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JOURNAL of PALEONTOLOGY

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JOURNAL OF PALEONTOLOGY, VOL. 9, NO. 1, PP. 3–5, PL. 1, JANUARY, 1935

YOUNG STAGES OF THE DEVONIAN TRILOBITE *DIPLEURA DEKAYI* GREEN[1]

G. ARTHUR COOPER
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ABSTRACT

Numerous specimens, ranging from 8 to 19 millimeters in length, show that the head of *Dipleura dekayi* Green attains adult characters when the individual is from 11 to 14 millimeters long; the pygidium, when the individual is from 20 to 40 millimeters long.

This paper describes a remarkable lot of specimens of the young of the trilobite *Dipleura dekayi* Green. Segmentation of the head and lobation of the tail in young *D. dekayi* have long been known but the new material is worthy of description because of the large number of specimens represented, the perfection of preservation of the specimens, and a few details hitherto unfigured in the young. Besides, the figures here reproduced are actual photographs illustrating anatomical details better than earlier figures.

The material consists of 90 specimens, representing seventy individuals ranging in length from 8 to 19 millimeters. One adult, probably 100 millimeters in length, was found with the young specimens. The material is from the University Quarry, on the campus of Colgate University, Hamilton, New York. The stratigraphic horizon represented is the Colgate member of the Skaneateles formation of the Hamilton group. The trilobites are imbedded in a soft sandy shale abounding in plant fragments and the small crinoid *Charientocrinus? cooperi* Goldring. The shale occurs as lenses in rather coarse, moderately heavy bedded and cross-bedded sandstone.

Most of the material belongs to Colgate University and was collected from a single block of shale by the writer in 1925. Four specimens were deposited in the Peabody Museum of Natural History, Yale University, and five of the figured specimens are in the National Museum, cat. nos. 88502 and 88503.

[1] Manuscript received June 2, 1934.

DIPLEURA DEKAYI Green
Plate 1

The adult.—Dipleura dekayi is abundant in the shaly sandstones and sandy shales of the Hamilton group in central and eastern New York. It is rare in western New York. The species is particularly abundant in eastern Onondaga and Madison Counties at the base of the Delphi member of the Skaneateles formation. Although this species is most abundant at this level, it occurs scattered throughout the mass of the Hamilton sediments, and occasionally in higher

beds. Adult *D. dekayi* is a large and unique trilobite, averaging about 6 inches in length but attaining 9 inches in individual examples. The most characteristic features of the genus, of which *D. dekayi* is the type species, are the absence of segmentation of the glabella, loss of the thoracic axial lobe, and complete loss of segmentation and annulation of the pygidium. Young specimens resemble *Calymene* strongly in having the axis well developed on the thorax and tail and in having a strongly segmented glabella.

The young.—The young specimens that form the subject of this paper are in the late neanic and early ephebic stages. The smallest specimen is 8 millimeters long and the largest is 19 millimeters long. The smallest specimen has thirteen thoracic segments, which is the full complement for the adult, but exhibits no other adult features. The ephebic stage is apparently only partially attained in the largest specimens from the Colgate Quarry, because strong segmentation and annulation of the tail are visible. A specimen from the middle Ludlowville formation, found near Randallsville, Madison County, New York, and measuring about 25 millimeters in length, has nearly the characteristics of an adult (see Pl. 1, figs. 18, 19, and 21).

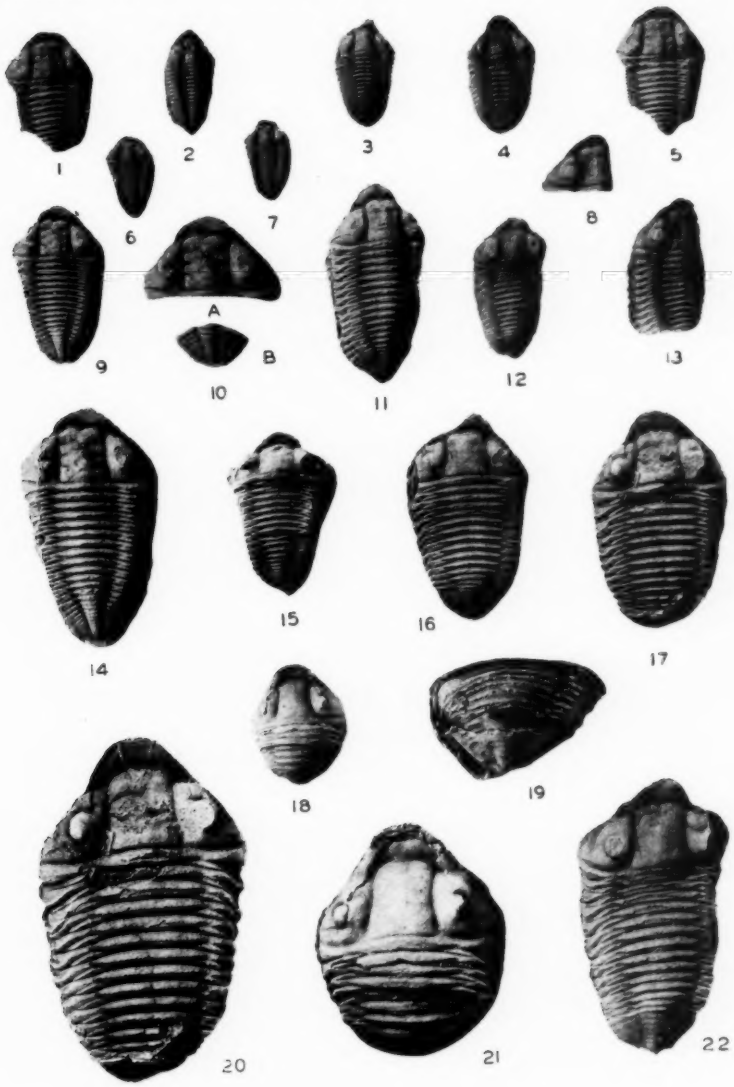
Fifteen specimens, ranging in length from 8 to 12 millimeters, show segmentation of the glabella. Three pairs of short, oblique furrows define four pairs of unequal lobes. The first glabellar lobe is the largest, the fourth is next in size, and the second and third are smaller but about equal. In specimens more than 12 millimeters in length segmentation of the glabella is partly or wholly lost. Two specimens 14 millimeters in length show the second and third furrows only. After a length of 11 to 14 millimeters has been attained the glabella becomes smooth, which is the adult feature of the head of *Dipleura*. The change from the neanic segmented glabella to the adult smooth glabella thus takes place when the individual has reached a length of eleven to fourteen millimeters.

Specimens having glabellar furrows

EXPLANATION OF PLATE 1

FIGS. 1–22—*Dipleura dekayi* Green. 1–17, 20, 22, Young individuals from the Skaneateles formation (Colgate member), University Quarry, Colgate University, Hamilton, Madison County, New York; 18, 19, 21, adult from lower Ludlowville formation near Randallsville, Madison County, New York. 1, 5, Individual, ×2, showing three glabellar furrows and broad thoracic axial lobe (figure 1 retouched), Colgate University specimen; 2, 11, nearly complete specimen 13.5 mm. long having a smooth glabella (fig. 2, ×1; fig. 11, ×2), Colgate University specimen; 3, 16, a specimen about 15 mm. long with smooth glabella, wide thoracic axis but well segmented and annulated tail (fig. 3 ×1; fig. 16 ×2), Colgate University specimen; 4, 17, 20, fine specimen about 17 mm. long having all adult characters except lobate and annulated tail; the impression of the borders of the epistomal plate on the upper surface of the test is well shown (figs. ×1, ×2, and ×3, respectively), U. S. N. M. cat. no. 88502a; 6, 7, 9, 10, 14, specimen 10.5 mm. in length showing neanic features; the glabella has three furrows; the thoracic axis is narrow; and the lobation and annulation of the tail are strong (figs. 6 and 7 are the same, fig. 6 being retouched, ×1; fig. 10a is the head ×3, retouched to show glabellar furrows; fig. 10b is the tail, retouched, ×3; fig. 9, ×2; fig. 14, ×3), U. S. N. M. cat. no. 88502d; 15, small specimen, ×2, showing thorax, Colgate University specimen; 8, 13, specimen, ×2, showing two glabellar furrows only (fig. 8, the head, retouched), U. S. N. M. cat. no. 88502b; 12, 22, rather large young specimen, 19 mm. long, with smooth glabella; pygidium is losing the strong axis (fig. 12, ×1; fig. 22, ×2), U. S. N. M. cat. no. 88502c. 18, 19, 21, a specimen about 25 mm. long showing smooth glabella (fig. 18, ×1; fig. 21, ×2); fig. 19 shows the tail of the same individual; the axial lobe is present, but pleurae and annulae are nearly obsolete, ×2; U. S. N. M. cat. no. 88503.

(p. 3)



Cooper, Young Dipleura dekayi

commonly have a strong indentation in the center of the front margin of the glabella. One specimen preserves a crescentic eye, the lenses of which are not very numerous. Many specimens, through the squeezing of the upper and lower parts of the test together during fossilization, exhibit the outlines of the epistomal plate impressed on the upper surface of the test. This feature is shown in Pl. 1, fig. 20.

In the youngest specimens, those with glabellar furrows, the axis of the thorax is rather narrow. In a specimen 8 millimeters long and 4 millimeters wide, the axis is about 1.5 millimeters wide. In another 11 millimeters long and 5.5 millimeters wide it is a little more than 2 millimeters in width. With increasing age the axis becomes wider, a specimen 19 millimeters long and 9 millimeters wide having an axis measuring 6 milimeters.

In the smallest and youngest specimens the axis of the pygidium is prominent, narrow, and tapers to a blunt point. The axis and strong annulations are visible in all young up to 19 millimeters in length but the contours are softer and the segmentation more subdued in the larger specimens. A specimen 25 millimeters in length, from the Ludlowville, shows lobation indistinctly, and annulation has almost completely disappeared. A specimen 40 millimeters in length, from the Mottville member of the Skaneateles formation at a locality northeast of Hamilton, shows full adult characters. Although not quite conclusive, these data suggest that full adult characters in the pygidium are attained by specimens between 20 and 40 millimeters in length.

Measurements of the Specimens Figured

Figure	Length mm.	Width mm.	Width of axis mm.
6	10.5	5	2.5
15	11.5	6	3
2	13	6.5	3.5
3	15	7.5	4.5
4	17	8.5	6.5
12	19	9.5	6.5

Measurements of Unfigured Specimens

Length mm.	Width mm.	Width of axis mm.	
8	5	2	Glabella segmented
9	6	2.7	Glabella segmented
9.5	6	3	Glabella segmented
12	6	3.7	Glabella segmented
13	6.5	3	Glabella smooth
16.5	9	5	Glabella smooth
18	8	4.7	Glabella smooth

Summary.—The above data indicate that adult characters are reached in the head of *Dipleura* when the individual reaches a length of 11 to 14 millimeters. Adult characters are attained by the pygidium when the individual has reached a length of 20 to 40 millimeters. The proportion of length to width, which is two to one in the adult, is the same in the young.

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A MIDDLE DEVONIAN BRANCHIOPOD FROM PERRY COUNTY, PENNSYLVANIA[1]

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ABSTRACT

Schizodiscus, a branchiopod long known in New York, is now known in Pennsylvania by a new species, *S. antecrenulus*.

Branchiopods of the genus *Schizodiscus* were first recorded from the upper Hamilton in central New York by J. M. Clarke[2] in 1888. In spite of the fact that the genus has been known for so many years it has only recently been found in Pennsylvania.[3]

The three specimens described below were found in the summer of 1932 near New Bloomfield, Pennsylvania, where the writer was engaged in a study of the rocks of the New Bloomfield quadrangle.

SCHIZODISCUS ANTECRENULUS Cleaves, n. sp.
Plate 2, figures 5–7

Carapace ovate in outline; greatest length along the hinge-line; greatest width just behind the beaks and slightly anterior to the center of the shield. Measurements of the three shields show that when the valves are fully expanded the widths and lengths are: 12 mm. and 16 mm., 8 mm. and 11 mm., and 6.5 mm. and 8 mm. The width is therefore about three-fourths of the length. All three specimens show the valves in contact along the hinge, but spread horizontally. The valves of one are slightly compressed laterally.

The surface is gently and regularly convex, elevated at the beaks, which are anterior, about one-third of the length of the carapace distant from the anterior end. Toward the hinge their slope is abrupt, leaving the hinge-line slightly depressed.

Hinge long and straight, extending the entire length of the carapace and showing no articulatory teeth or ridges.

The ventral margin is gently recurved and slightly thickened.

The surface ornamentation consists of continuous, concentric, sharp ridges, closely crowded near the apices and more distant on the posterior portions of the valves. Twenty-eight to thirty of these ridges may be counted on the mature individuals. The anterior portion of each valve in front of the apex is regularly crenulated by transverse ridges. In the largest specimen collected each crenulation occupies 0.5 mm.

Observations.—This interesting species is very similar to *Schizodiscus capsa* Clarke. The only apparent difference is the crenulation of the concentric ridges on the anterior portion of the valves and in the slightly larger number of ridges in the mature specimen.

Occurrence.—Three specimens of the species have been obtained, all from a single locality, at Barnett's Mill (three-fourths of a mile southeast of New Bloomfield, Perry County) in the highly fossiliferous Moscow shale of the Hamilton Group.

The specimens have been deposited in the collections of the Museum of Comparative Zoology, Cambridge, Mass. Holotype, cat. no. 1982; paratypes, cat. nos. 1983, 1984.

[1] Manuscript received January 3, 1934.

[2] Hall, J., and Clarke, J. M., *Natural history of New York, Paleontology*, vol. 7, pp. 207–208, pl. 35, figs. 1–9, 1888.

[3] Willard, B., and Cleaves, A. B., Hamilton group of eastern Pennsylvania: *Geol. Soc. Am., Bull.*, vol. 44, pp. 757–782 (cf. faunule 26, p. 775), 1933.

JOURNAL OF PALEONTOLOGY, VOL. 9, NO. 1, PP. 7–9, PL. 2, JANUARY, 1935

AN UNRECORDED STRUCTURE IN CERTAIN SEMIRETICULATE *PRODUCTI*[1]

GEORGE H. GIRTY
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ABSTRACT

Several species of *Producti* of the semireticulate group possess a partition in the pedicle valve that passes obliquely outward from the beak and shuts off the auriculation. Its function is that of a hinging structure.

To imply that any structural feature in any species of *Productus* is unrecorded is open to challenge, for the literature dealing with these shells has become so extensive that it is impossible to read it all and do much else. In this instance it may at least be said that the structure appears to be unrecorded for any of the species which the statement directly concerns.

The structure in question, or rather its effects, first came to my notice when in 1900 or thereabouts I attempted to chip the rock from those large *Producti* to which I later gave the name *P. hermosanus* and *P. coloradoensis*. It seemed to be almost impossible to uncover these shells without breaking off the auriculations, though the reason for the ensuing casualties was not recognized until a number of years later. The reason consists of what seems to be a vertical partition of shelly material on the inside of the pedicle valve, beginning near the beak and passing obliquely outward, shutting off the auriculations. This structure, which forms a plane of dehiscence such than an ill-directed blow causes the auriculation to part company with the rest of the shell, is definitely related to a conspicuous feature of external configuration; namely, an arching row of spines on the side of the valve just above where the auriculations may be said to begin. The spines are regularly spaced and show a regular increase in size, the final ones being extremely large. The spines thus signalized by their size and alignment commonly give rise to or are associated with a ridge which they surmount and the ridge commonly descends abruptly on the outer side to form a conspicuous groove. When the auriculation splits off in the manner above described, the row of spines is left on the side of the vault.

The function of the ridge is not probably to shut off the auriculation from the interior of the shell but to serve as a hinging structure. I have observed what seems to be a corresponding ridge on the inside of some

[1] Published by permission of the Director of the U.S. Geological Survey. Manuscript received October 16, 1934.

brachial valves, and although it would be difficult to prove that the two structures interlocked, it seems probable that they did so. If this is true, it disposes of the hypothesis that the plane of dehiscence is merely the lateral surface of a deposit of callus thickening the auricles, an hypothesis which possessed slight probability to begin with.

It is somewhat surprising to find in these large semireticulate shells a structure which recalls the submarginal ridge distinctive of the genus *Marginifera*, but apparently it is homologous in the degree in which it is developed at all, though of course the line of development is carried much farther in such species of *Marginifera* as *M. splendens* and related species. A still further parallel can be drawn between *M. splendens* and these large *semireticulati*, for *M. splendens* shows a marked tendency to develop two oblique rows of spines comparable in character and position to those which I have described. This feature, however, is not as constant in *M. splendens* nor by any means as conspicuous, for it is not associated with any corresponding deflection of the surface. Nevertheless when once recognized it can be observed again and again, and becomes significant through repetition. Though not mentioned by Dunbar and Condra[2] it is in my specimens much more persistent and certainly more significant than the irregular transverse row across the middle of the anterior slope cited in their description.

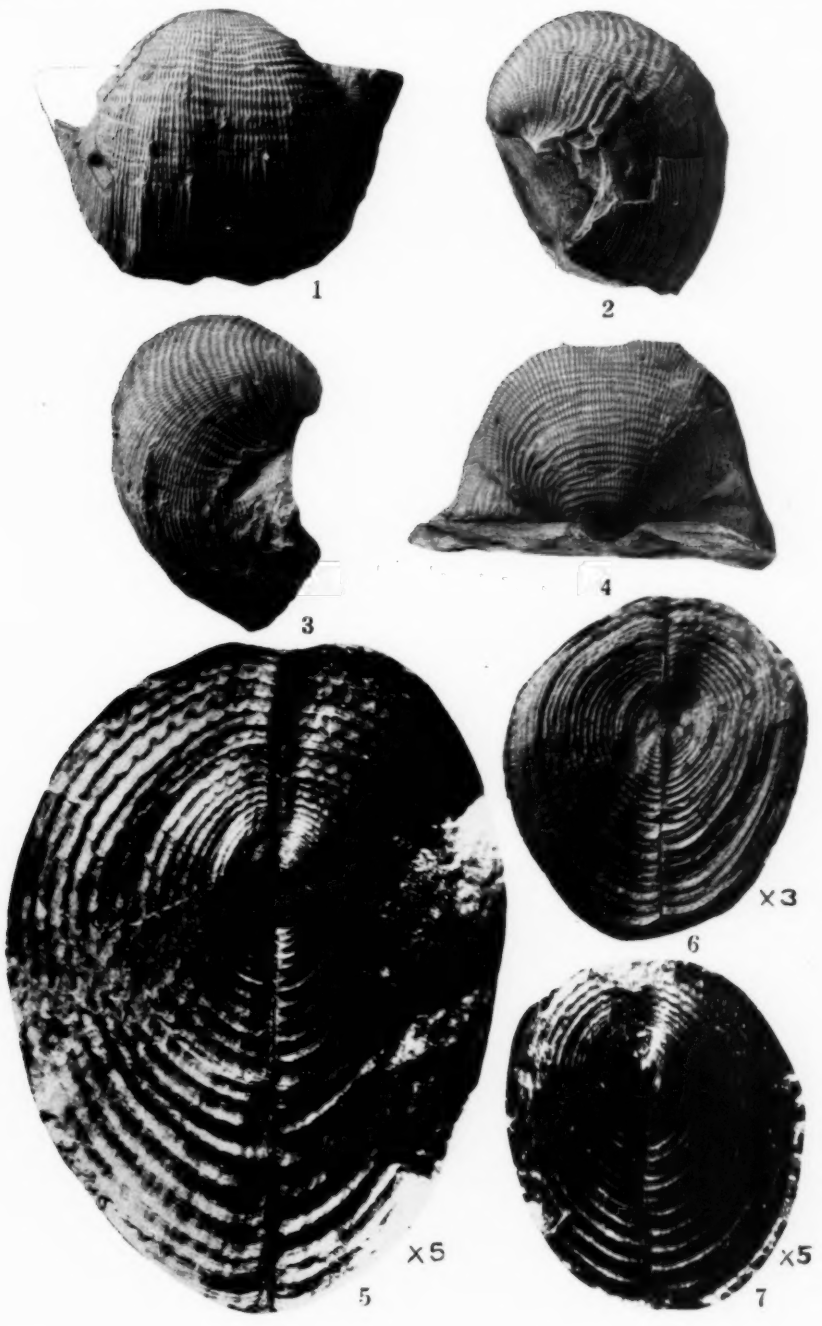
It seems probable that the pres-

[2] Dunbar, C. O., and Condra, G. E., Brachiopoda of the Pennsylvanian system in Nebraska: *Nebraska Geol. Survey*, ser. 2. Bull. 5, pp. 228–232, 1932.

EXPLANATION OF PLATE 2

FIGS. 1–4—*Productus coloradoensis* Girty, a specimen from the Cherokee formation collected by E. J. Palmer from a mine dump near Carterville, Missouri. 1, The pedicle valve seen from above. The auriculation at the right is intact; the auriculation at the left is broken off along a vertical plane formed by an internal ridge or partition. 2, Specimen viewed obliquely from one side showing the broken auriculation. The vertical surface of the break (it really slopes somewhat inward from above) is faced with a coating of shell and is a clean fracture along an internal partition. 3, A corresponding oblique view of the opposite side showing more clearly the unbroken auriculation with its deep groove surmounted by a spiniferous ridge. The spines (as represented by their scars) are not as large in this specimen as in many. 4, Posterior view. At the left is a deep groove defining the auriculation and above it on the side of the vault a sharp ridge surmounted by a row of spines. The broken auriculation at the right is in shadow and its characters are obscured. These first spines are small, those farther down the row are much larger. The brachial valve is also present in this specimen, though it is without evidence save for an edge sharing in the break. All figures natural size. (p. 7)

5–7—*Schizodiscus antecrenulus* Cleaves, n. sp., Moscow shale of the Hamilton group at Barnett's Mill, ¾ mile southeast of New Bloomfield, Pa. 5, the holotype, largest of the three specimens (×5); valves slightly compressed laterally; crenulations of the ridges very distinct on the anterior portion of the valves (M. C. Z. cat. no. 1982). 6, Fully expanded valves, (×3) showing well-developed continuous concentric ridges, crowded near the apices; crenulations faintly discernable on the anterior portion (M. C. Z. cat. no. 1983). 7, The smallest specimen (×5) showing faint beginnings of the crenulation of the ridges on the anterior portion (M. C. Z. cat. no. 1984). (p. 6)



Girty, New structure in Producti
Cleaves, New branchiopod

ence of this internal structure with its expression on the exterior in the form of a spiniferous ridge on each side of the vault above the auriculations will serve to define a compact group of *Producti* in the semireticulate stock, for the character, though varying in degree, seems to be extremely constant. On these grounds the group would include *P. hermosanus*, *P. coloradoensis*, *P. morrowensis*, and probably *P. portlockianus*, together with other species.

As regards *P. portlockianus*, Dunbar and Condra describe the spiniferous ridge at the base of the vault, but not the internal partition which seems regularly to accompany it. The form which they identify with *P. portlockianus* is well known to me and it certainly has the deciduous auriculations of this group. I have been identifying it, however, not with *P. portlockianus* but with *P. hermosanus*, so that if they are right and I also am right, *P. hermosanus* is a synonym of *P. portlockianus*. Dunbar and Condra identified their form with *P. portlockianus* on the strength of its abundance at one of the original localities, but they note that it does not agree very well with Norwood and Pratten's figures. I have been interpreting *P. portlockianus* differently and because it does agree with the original description and figures I have so identified a species from the Cisco formation of Texas; that species I believe to be distinct from *P. hermosanus*.

The specimen which is here employed to illustrate the structure described above was collected in the Pennsylvanian strata of southwestern Missouri. It is regarded as belonging to *P. coloradoensis*, and though it differs in a number of details from the type specimens, the differences do not at present seem sufficient to distinguish it as another species. This specimen is rather apt for the present purpose because it is intact on one side but on the other has lost the auriculation by cleavage in the manner that I have attempted to describe. The auriculation at the right is unbroken and is defined by a conspicuous groove with a sharp ridge above it on the side of the vault. The row of spines surmounting the ridge is also conspicuous, but the spines are not as large as in the type specimens of *P. coloradoensis*. The auriculation on the other side is broken off and clearly shows the internal partition which determined the plane of cleavage. This plane is not merely the side of the ridge from which the spines are developed, though it is partly that.

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FRESH-WATER MOLLUSKS FROM THE CATAHOULA SANDSTONE (MIOCENE) OF TEXAS[1]

F. STEARNS MACNEIL
U. S. Geological Survey, Washington, D.C.

ABSTRACT

A Miocene fresh-water fauna from the Catahoula sandstone of Texas is intermediate in type between those of the later Cretaceous and early Eocene on one hand and those of the Mississippi drainage basin of today on the other hand. It helps to fill a gap in the sequence of fresh-water faunas now known. Two new genera and 5 new species of the Unionidae are described and certain other forms are noted.

This paper deals with an unusual fresh-water fauna represented by a well preserved collection forwarded to the United States Geological Survey by Mr. Leslie Bowling and Mr. John C. Myers while in the employ of the Roxana Petroleum Corporation, and upon an additional collection made by Mr. Bowling at the request of the United States Geological Survey.[2]

The Catahoula sandstone fauna is interesting because it fills in a gap between the Recent fauna of the Mississippi drainage system and the fauna of the later Cretaceous and early Eocene. The Mississippi contains without doubt the most abundant and diverse fauna existing anywhere in the world today, but many of the types of mussels in it are not represented in any of the Tertiary fresh-water faunas from the interior of the continent. It is, therefore, significant but not strange that certain of these types should be present in the Catahoula sandstone. Biologically these shells are of a type intermediate between the later Cretaceous and the Recent forms and enable us to see with more certainty which of the former were the precursors of the latter.

Some of the Catahoula types, however, are, so far as known, peculiar to it and one unique genus to be described is not definitely related to any other forms represented in the recent or fossil collections in the United States National Museum.

[1] Published by permission of the Director of the U.S. Geological Survey. Manuscript received January 1, 1934.

[2] A preliminary report, based on the insufficient material of the first collection, entitled *A new genus of fresh-water mussel from the Catahoula sandstone of Texas*, was read at the March, 1932, meeting of the American Association of Petroleum Geologists. Unfortunately some tentative new names used in that report were cited by Bowling and Wendler (Study of the Catahoula formation: *Bull. Am. Assoc. Petrol. Geol.*, vol. 17, pp. 526–547, May, 1933). These names are not being used; thus *Amblemoidea elaboratus*, *A. bowlingi*, and *A. catahoulensis* have no status, and the forms for which they were used are referred to different genera and described in this paper under different names. *Lampsilis bowlingi* in this paper is not the *Amblemoidea bowlingi* cited by Bowling and Wendler.

The author gratefully acknowledges the generous and constructive criticism of Mr. William B. Marshall of the United States National Museum, who was frequently consulted and was greatly interested in the progress of this paper.

THE CATAHOULA SANDSTONE

The Catahoula sandstone is a nonmarine formation. Evidences of deposition under fresh-water, estuarine and lagoonal conditions have been recognized by most of those who have studied it.[3] The sediments consist of clays, fine conglomerates and crossbedded layers of fine and coarse sand, in places filled with clay balls. At intervals lenticular members bearing fresh-water molluscan shells indicate the existence of lakes and rivers on this ancient coastal plain.

The present outcrop of the formation parallels the shore-line of the Gulf of Mexico in the form of an arc extending from Alabama to Texas, where in the vicinity of the Guadelupe River it grades laterally into the Catahoula tuff.

In Alabama the formation grades into clayey sands and varicolored joint clays which Cooke, in 1929, tentatively correlated with the Tampa limestone of lower Miocene age.[4] The stratigraphic position of the formation in central and eastern Texas gives little indication of its exact age. It lies unconformably above the Fayette sandstone of Jackson (upper Eocene) age, and is overlain unconformably by the Oakville sandstone of late middle and early upper Miocene age. The collection of fossils described in this paper is from the western part of the Catahoula sandstone just east of the zone of its transition into the Catahoula tuff.

ORGANIC REMAINS

The Catahoula sandstone is characterized by a great scarcity of organic remains. Those known are mostly leaves and wood which, in some places are in sufficient quantity to form thin beds of lignite. Animal remains in the formation are restricted to some unidentifiable bones and some peculiar fresh-water mollusks. Meyer,[5] in 1886, noted the occurrence of several species of fresh water bivalves at Grand Gulf, Miss., but if these specimens were collected they were never described. G. D. Harris, in 1901, collected some specimens of Unionidae from a 6-inch layer of fine gray clay at the Chalk Hills, near Rosefield, La. Descriptions and figures of these fossils were included by Miss Maury in her report on *The Oligocene of the Southern United States*.[6] Miss Maury's types, which now repose in the Harris collection at Ithaca, New York, were examined by the writer and the fauna was found to agree closely with the one here described from Texas, although minor specific differences were noted.

The genera of mussels in the Catahoula sandstone are distinctly unre-

[3] See Matson, G. C., The Catahoula sandstone: *U. S. Geol. Survey, Prof. Paper* 98, pp. 209–226, 1916.

[4] Cooke, C. W., and Mossom, Stuart, Geology of Florida: *Florida Geol. Survey, Twentieth Ann. Rept.*, p. 79, 1929.

[5] Meyer, Otto, Observations on the Tertiary and Grand Gulf of Mississippi: *Am. Jour. Sci.*, 3d ser., vol. 32, p. 25, 1886.

[6] Maury, C. J., *Bull. Am. Paleontology*, vol. 3, No. 15, p. 17, p. 29, 1902.

lated and probably represent a variety of sources from which the Catahoula fauna was derived. The specific differences between the Texas and Louisiana collections are of the degree to be expected in streams separated by over 300 miles and with probably independent mouths on the ancient gulf.

The fossils are preserved as molds and those available to Miss Maury were exceedingly poor. Those from Texas, however, are in a hard bluish-gray quartzitic sandstone from which impressions were easily taken. In addition to the mollusks described here, there were abundant remains of monocotyledonous plants, a turtle bone and an alligator tooth.

The exact locality from which the fossils were taken was given by Mr. Myers as

> 5 miles north of the town of La Grange [Fayette Co., Texas], about one-half mile northwest of the south corner of the James Green League. The fossils were found in the upper part of a quartzitic sandstone which is developed only locally about 30 to 40 feet above the base of the Catahoula formation as described after Alexander Deussen, [U. S. Geol. Survey] Professional Paper 126.

This collection has received U. S. G. S. station number 12676.

The species described from Texas in this paper are:

Costanaia arciformis MacNeil, n. gen. and sp.
Megalonoidea porcata MacNeil, n. gen. and sp.
Megalonoidea rugicosta MacNeil, n. sp.
Undetermined members of the *Quadrula* group
Elliptio cornelliana (Maury)
Lampsilis marshalli MacNeil, n. sp.
Lampsilis bowlingi MacNeil, n. sp.
Sphaerium sp. cf. *S. rugosum* Meek
Musculium sp. ind.
Helisoma sp. ind.

To these may be added the forms described by Miss Maury from Louisiana:

Costanaia trigoniaformis (Maury)
Elliptio cornelliana (Maury)
"Unio" cretacollis Maury

SYSTEMATIC DESCRIPTIONS

Family UNIONIDAE
Subfamily UNIONINAE Swainson, 1840

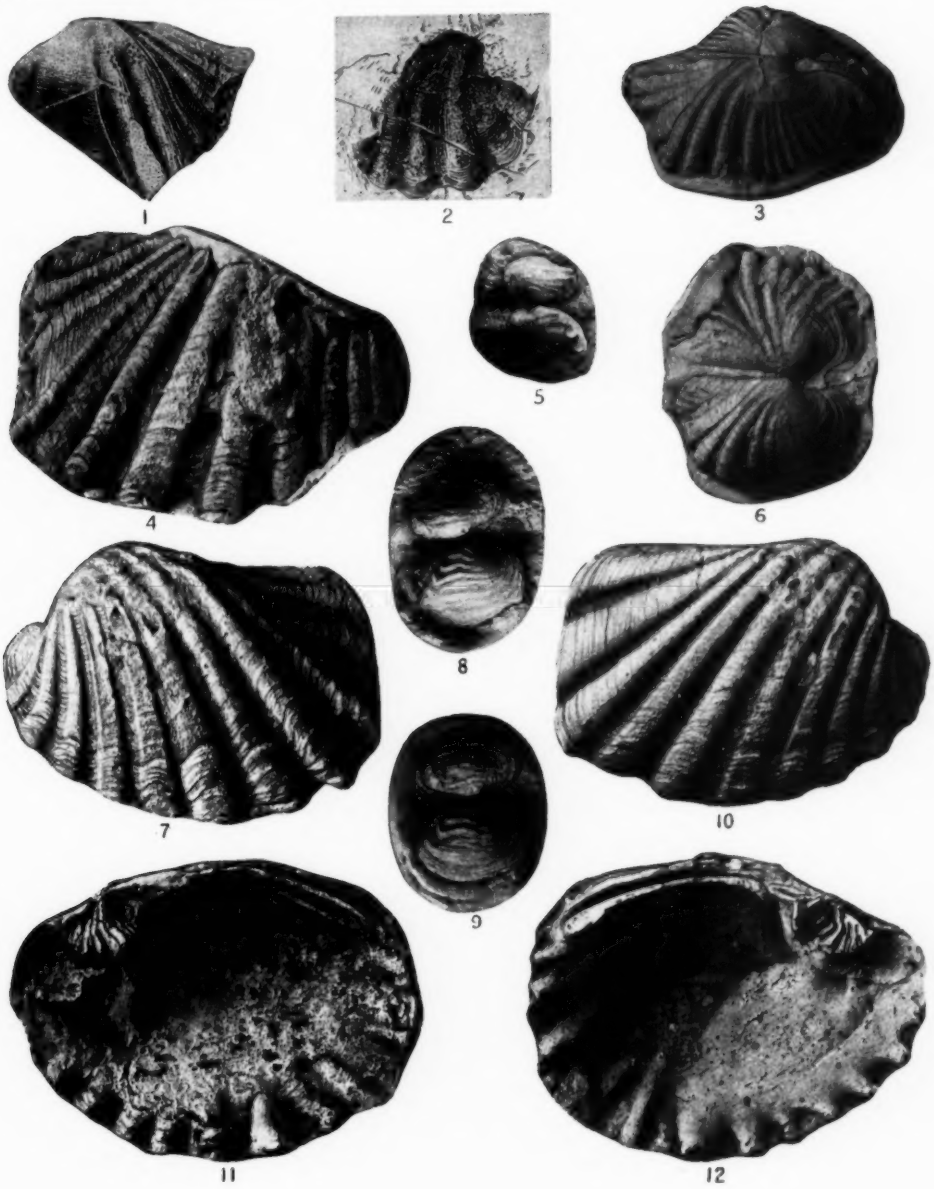
COSTANAIA MacNeil, n.gen.

Shell subquadrate and inflated, higher posteriorly than anteriorly. Beak sculpture semiconcentric, sometimes broken and often indistinct or wanting anteriorly, produced posteriorly on the umbonal ridge as small downward-pointing chevrons. Valves sculptured with heavy, nonbifurcating radial ribs which do not extend to the beak, those of the posterior region being much the larger. Shell thicker anteriorly than posteriorly. Pseudocardinals massive and deeply schizodont, two widely separated teeth in the left valve, one large tooth in the right valve. Laterals single in the right valve, double in the left valve.

EXPLANATION OF PLATE 3

FIGS. 1, 2—*Costanaia trigoniaformis* (Maury), copies of Miss Maury's figures of the types, reduced one-fourth. (p. 12)

3–12—*Costanaia arciformis* MacNeil, n. sp. 3, 6, Two young individuals (paratypes), ×1½; 4, fragment of a right valve showing variation in ribs of the posterior slope for contrast with fig. 10, ×¾; 5, 8, 9, impressions of beak sculpture, ×3; paratypes, U. S. N. M. cat. no. 371925. 7, 10. Right and left valves of the holotype, ×¾; U. S. N. M. cat. no. 371926. 11, 12. Casts of the interior of another specimen showing hinge, ×¾; paratype, U. S. N. M. cat. no. 371925. (p. 13)



MacNeil, Miocene mollusks

Type species, *Costanaia arciformis* MacNeil, n. sp.

Type locality: 5 miles north of La Grange, Fayette County, Texas. U. S. Geological Survey station no. 12676.

This genus is remarkable for its radial ribbing. *Unio? trigoniaformis* Maury is clearly related to the type species and it is not difficult to see Miss Maury's reason for the statement that "In some respects this shell recalls the South American genus *Castalia*." However, the ribs do not originate at the beak as in the Hyriinae, and the discovery of concentric beak sculpture at once places these shells with the Unioninae. So far as known, *Costanaia* occurs only in the Catahoula sandstone. Neither the fossil nor recent collections in the United States National Museum contain any close relatives of this genus.

COSTANAIA ARCIFORMIS MacNeil, n. sp.
Plate 3, figures 3–12; Plate 5, figures 14, 15

Shell subquadrate and much inflated, the posterior margin nearly straight, ventral margin arcuate, curving rapidly to a sharply rounded anterior dorsal angle; hinge line moderately long and broadly arcuate; lunule well defined; beaks high and situated well into the anterior third of the shell; beak sculpture fine semiconcentric undulations, often incomplete anteriorly, pointing down the umbonal ridge as small raised chevrons, and striking back sharply on the posterior slope to the umbo; valves elaborately sculptured with from 12 to 15 strong radial, broadly rounded, nonbifurcating ribs, most pronounced and originating nearer the beak in the vicinity of the umbonal rostrum, usually one rib on the posterior slope originating nearly at the umbo; width of ribs variable, either valve having wider ribs on the posterior slope, the other valve with corresponding furrows; margin deeply crenulated by ribs and interspaces; posterior dorsal region often fluted; anterior muscle scar deep and rough, posterior scar indistinct.

Holotype (U. S. N. M. cat. no. 371926), external mold of a pair of valves, measures: Length, 68 mm.; height, 53 mm.; convexity, 23 ± mm.; thickness, 45 ± mm.

Paratypes (U. S. N. M. cat. no. 371925), molds of interior of both valves, two juvenile individuals, three beaks, a fragmental right valve and a right valve hinge.

In gross appearance this species suggests a large *Arca* or *Cardita* rather than a fresh water mussel.

An examination of the type of *C. trigoniaformis* (Maury) shows that it is a broken subquadrate shell and not triangular in form as supposed by Miss Maury. It is smaller than *C. arciformis* and averages only one-half to three-fourths as many ribs as the latter. Miss Maury's figure 6, which she identified as *Anodonta cornelliana* Maury, is more probably the young of *C. trigoniaformis*.

MEGALONOIDEA MacNeil, n. gen.

Shell large and subquadrate, moderately to much inflated. Beak sculpture consisting in the youngest stage of semiconcentric, doubly looped undulations, the anterior loop being the largest, the posterior loop becoming more acute and elongate in advanced stages to form straight or wavy chevrons pointing down the umbonal ridge. Adult sculpture consisting of heavy diagonal posterior plications originating as the anterior side of the umbonal chevrons and a smaller anterior set of plications which form a conspicuous angle with the large posterior plications. Pseudocardinals fairly heavy; left valve with pronounced posterior process, elongate anterior dorsal ridge and anterior ventral socket; right valve with a large slightly anteriorly inclined tooth and behind it a wide but shallow socket. Laterals long and arcuate, single in the right valve and double in the left valve.

Type: *Megalonoidea porcata* MacNeil, n. sp.

Type locality: 5 miles north of the town of La Grange, Fayette County, Tex. U. S. Geological Survey station no. 12676.

The nearest relative of *Megalonoidea* is a form (Pl. 4, fig. 1) collected from the Bear River formation, of Upper Cretaceous age, 1 mile east of Waterfall station, Wyo., and identified by T. W. Stanton as *Unio* (*Loxopleurus*) *belliplicatus* Meek.[7] It is an end member of that variable species, being shorter and higher and with straighter ribs than the typical form.[8]

The name *Loxopleurus*[9] is, of course, entitled to generic rank.

This genus presents all the general characters displayed by *Megalonoidea* except in the development of the anterior ribs. The umbonal chevrons of *Loxopleurus* are also longer, more numerous, and more acute. Record of a form with such kindred characters to *Loxopleurus* in lower Miocene strata is of especial interest, since White[10] considered *L. belliplicatus* to be without progeny in post-Bear River times. If *Megalonoidea* can be considered an intermediate form, it is not at all difficult to see foreshadowed in these early plicate Naiades such Recent genera as *Megalonaias* and *Amblema*. On Plate 4 is shown a comparison of photographs of *Loxopleurus belliplicatus*, the two species of *Megalonoidea*, and the Recent *Amblema costata* Rafinesque. The striking development of two sets of plications and the posterior migration of the angle which they form can hardly be overlooked.

[7] *Unio* (*Loxopleurus*) *belliplicatus* Meek, Meek, F. B., *U. S. Geol. Survey Terr., Second Ann. Rept.*, p. 294, 1871.

[8] Typical forms figured by Meek, F. B., Paleontology, Part 1: *U. S. Geol. Survey 40th Par., Rept.*, vol. 4, p. 165, p. 16, figs. 4, 4*a*, 1877; White, C. A., Review of the nonmarine fossil Mollusca of North America: *U. S. Geol. Survey, Third Ann. Rept.* (1881–82), pl. 6, figs. 1–3, 1883.

[9] *Unio* (*Loxopleurus*), Meek, F. B., Preliminary paleontological report: *U. S. Geol. Survey Terr. Fourth Ann. Rept.* (1870), pt. 4, p. 294, 1871.

[10] White, C. A., Ancestral origin of North American Unionidae: *Smithsonian Misc. Coll.*, vol. 48, p. 84, 1905.

MEGALONOIDEA PORCATA MacNeil, n. sp.

Plate 4, figures 2, 5, 6

Shell subquadrate and much inflated; posterior margin nearly straight; ventral margin strongly arcuate; lateral and ventral margins deeply crenulate; beaks high and situated at about anterior third of shell; beak sculpture consisting of semiconcentric undulations in youngest stages, becoming elongate and often angulated anteriorly in advanced stages and extending down the posterior ridge as coarse, blunt chevrons, the anterior side in the adult being produced ventrally as heavy diagonal folds; diagonal folds extremely heavy centrally, becoming horizontal or slightly dorsally inclined on the posterior slope; angle formed with anterior folds very far forward. Hinge teeth as described for the genus.

Holotype (U. S. N. M. cat. no. 371927), an external mold of a right valve and internal molds of both valves, measures: Length, 92 mm.; height, 75 mm.; convexity, 25 ± mm.

Paratypes (U. S. N. M. cat. no. 372542), two beaks, and an internal mold of a large specimen.

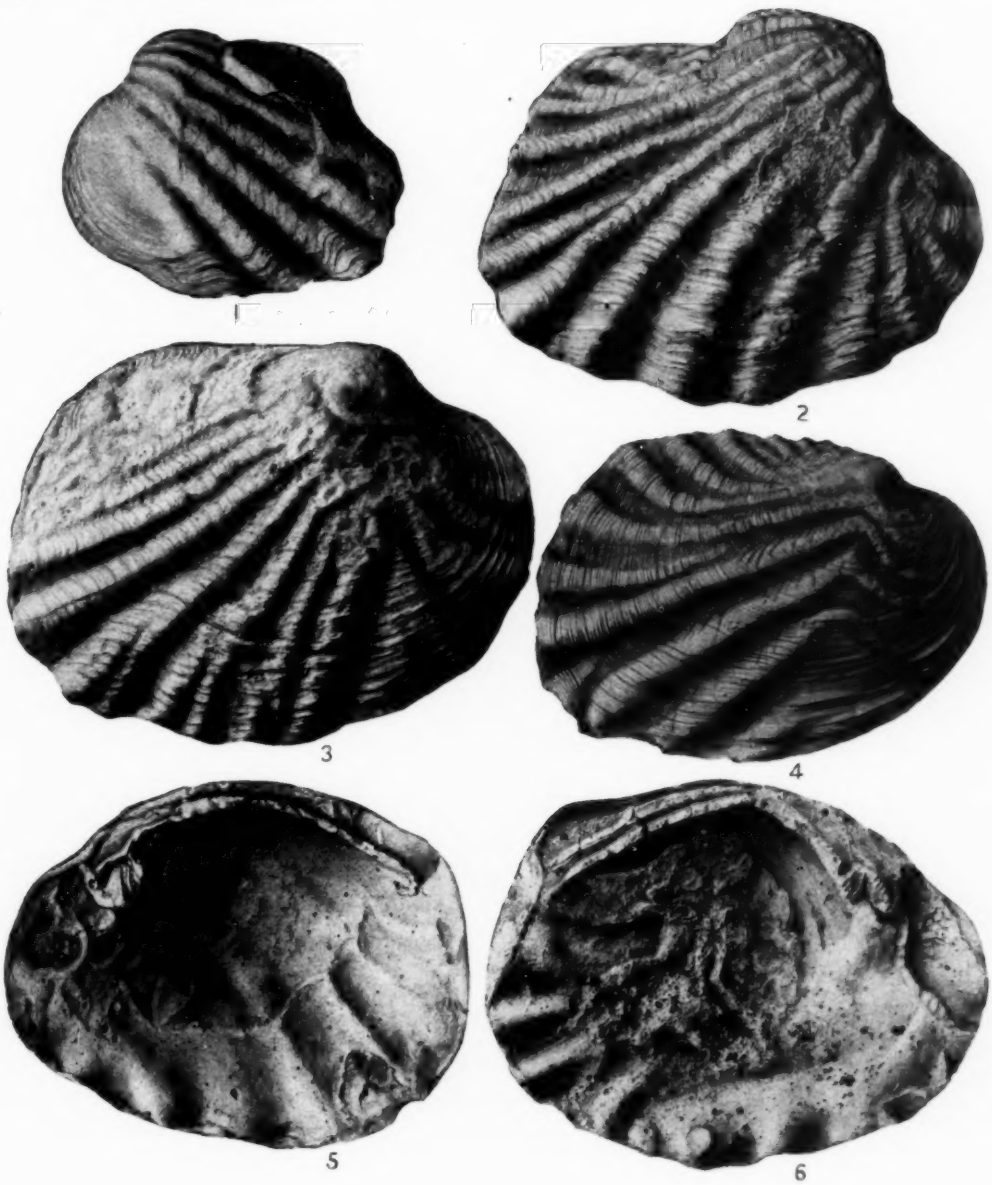
EXPLANATION OF PLATE 4

FIGS. 1—*Loxopleurus belliplicatus* Meek, ×¾, from the Bear River formation (Upper Cretaceous) of Wyoming for comparison with figures 2, 3, and 4. U. S. N. M. cat. no. 22271. (p. 14)

2, 5, 6—*Megalonoidea porcata* MacNeil, n. sp. 2, Exterior of holotype, ×¾, showing the anterior ribs and the indefinite angle between them and the midribs; 5, 6, interior of holotype, ×¾, U. S. N. M. cat. no. 371927. (p. 14)

3—*Megalonoidea rugicosta* MacNeil, n. sp., ×¾, showing a better developed and more posterior ribbing angle than in *M. porcata*. Holotype U. S. N. M. cat. no. 371928. (p. 15)

4—*Amblema costata* Rafinesque, ×¾, Recent, from Arkansas, showing an unusually fine development of divaricate ribbing. U. S. N. M. cat. no. 105125. (p. 14)



MacNeil, Miocene mollusks

MEGALONOIDEA RUGICOSTA MacNeil, n. sp.

Plate 4, figure 3; Plate 5, figures 3, 4

Shell subquadrate and somewhat inflated; posterior margin subtruncate, ventral margin more arcuate; anterior margin semicircular; ventral margin deeply crenulate, anterior margin only slightly so; beaks moderately high and placed at anterior third of shell; beak sculpture may be similar to that of *M. porcata;* adult posterior ribs moderately heavy, central ribs smaller and bifurcating, both being traceable to the wavy anterior loops of the beak; angle formed by anterior and mid ribs approximately under the beaks; pseudocardinals massive; laterals unknown but probably long.

Holotype (U.S.N.M. cat. no. 371928), external mold of a right valve and an internal mold of the left valve, measures: Length, 98 mm.; height, 78 mm.; convexity, 20+ mm.

M. rugicosta differs from *M. porcata* in several details. The mid-ribs of the latter are much heavier and the angle formed by the anterior and postior ribs is considerably more posterior in *M. rugicosta. M. porcata* is apparently the more inflated. The beak figured in Plate 5, figure 4, may belong to *M. rugicosta.* If so, the umbonal chevrons of this species are much more blunt than those of *M. porcata.*

UNIDENTIFIED SPECIMENS OF THE QUADRULA GROUP

In addition to the above, two more impressions of shells belonging to the *Quadrula* group were found. One is a specimen of beak sculpture (Pl. 5, fig. 5) having five widely separated concentric undulations, the two uppermost being sharply oblique, the middle one nearly horizontal, and the two ventralmost forming large, obtuse chevrons. The other specimen (Pl. 5, fig. 6) is a medium-sized plicate shell with rough upturned chevrons posteriorly and broken or zigzag sculpture anteriorly.

Genus ELLIPTIO Rafinesque

ELLIPTIO CORNELLIANA (Maury)

Plate 5, figures 8–10

Anodonta cornelliana MAURY, *1902.* Bull. Am. Paleontology, vol. 3, no. 15, p. 79, pl. 29, figs. 3, 5, 7 (not fig. 6).

Miss Maury described this species as follows:

> Shell elongate-oval, apparently thin and light. Posterior extremity prolonged and sharply pointed, anterior rounded. Posterior area defined by a sharp carina passing from the beak to the posterior extremity. Lines of growth delicately impressed. Beak rather prominent, placed at the anterior fifth of the shell. Beak sculpture concentric. Length of shell, 75 mm.; height, 30 mm.

An emended desciption including hinge characters follows:

Shell elliptical, anterior margin rounded, posterior margin drawn to a point, dorsal margin from the beak to posterior apex arcuate and unbroken; beaks low and pointed, strongly prosogyrate, and situated well in advance of the anterior fourth of the shell; beak sculpture concentric (Maury) but apparently not strong; growth lines faint in juvenile shell, becoming irregular in adult; posterior ridge long and arcuate, extending from beak to the posterior extremity and nearly paralleling dorsal margin; pseudocardinals smooth and antero-ventrally directed, double and nearly equal in left valve, right valve with strong ventral tooth and faint dorsal ridge; laterals long and arcuate, single in right valve and double in left valve.

Figured material (Plesiotypes, U. S. N. M. cat. no. 372857): One adult left valve, one juvenile right valve, and internal impressions of both valves.

Locality: Five miles north of La Grange, Fayette Co., Texas.

Dimensions of largest specimen: Length, 60 mm.; height, 30 mm.; convexity, 11 mm.

The newly acquired impressions of the hinge show this species to be an *Elliptic* and not an *Anodonta.* The arched dor-

sal margin and pointed posterior are its distinctive features.

The type, *Anodonta cornelliana* Maury is in the Harris collection at Ithaca, New York.

Type locality: Chalk hills, two and three-quarter miles south of Rosefield, La.

Genus LAMPSILIS Rafinesque

LAMPSILIS MARSHALLI MacNeil, n. sp.

Plate 5, figure 16

Shell subtriangular, much inflated; posterior margin nearly straight; ventral margin broadly arcuate; anterior margin sharply arcuate; posterior dorsal region strongly winged; hinge line with pronounced lunular depression; beaks moderately high, recurved over the lunule, and well in advance of mid-line; posterior slope marked off by a strong subangular umbonal ridge which dies out before reaching the margin; growth lines wide apart and distinct; pseudocardinals small, simple and oblique; laterals delicate and curved, single in right valve and double in left valve.

Holotype (U. S. N. M. cat. no. 372855), external and partial internal mold of a left valve, measures: Length, 76 mm.; height, 60 mm.; convexity, 23 mm.

Miss Maury's *Unio cretacollis* is too badly crushed to be definitely allied with this species, but certainly there is no indication of a pronounced sulcus in front of the posterior rostrum in the Texas form.

This species is very similar to the more truncate male specimens of the Recent *Lampsilis ventricosus* var. *satur* Simpson, which inhabits the waters of the southwestern Mississippi region as far west as the Sabine River. The only known early Tertiary species comparable to it is a form described by Conrad, from beds of questioned Eocene age in Colorado, as *Anodonta decurtata* Conrad.[11] A sketch later made of this species by White[12] strongly suggests that it likewise is a *Lampsilis*. *Lampsilis marshalli* is readily distinguishable from the above species by its conspicuous dorsal wing.

[11] Conrad, T. A., *Am. Jour. Conchology*, vol. 6, p. 200, pl. 11 fig. 6.

[12] White, C. A., Review of the nonmarine fossil Mollusca of North America: *U. S. Geol. Survey, 3d. Ann. Rept.* (1881–82), p. 479, pl. 29, figs. 27, 28, 1883.

EXPLANATION OF PLATE 5

FIGS. 1, 2—*Megalonoidea porcata* MacNeil, n. sp., ×1½, impressions of beak sculpture showing how it gives rise directly to the adult sculpture. Paratypes, U. S. N. M. cat. no. 372542. (p. 14)

3—*Megalonoidea rugicosta* MacNeil, n. sp., ×¾, cardinal area of the holotype. U. S. N. M. cat. no. 371928. (p. 15)

4—(?)*Megalonoidea rugicosta* MacNeil, n. p., ×1½, specimen with beak sculpture of blunt chevrons that may belong to this species. U. S. N. M. cat. no. 372544. (p. 15)

5, 6—Unidentified fragments probably related to the *Quadrula* group. U. S. N. M. cat. no. 372546. Fig. 5, ×1½; Fig. 6, ×¾. (p. 15)

7—*Musculium* sp., ×1½ resting on an eroded valve of *Costanaia arciformis*. U. S. N. M. cat. no. 372547. (p. 17)

8–10—*Elliptio cornelliana* (Maury), ×¾. 8, Juvenile right valve; 9, an adult valve showing arched dorsal margin; 10, impression showing hinge of a pair of valves; U. S. N. M. cat. no. 372857. (p. 15)

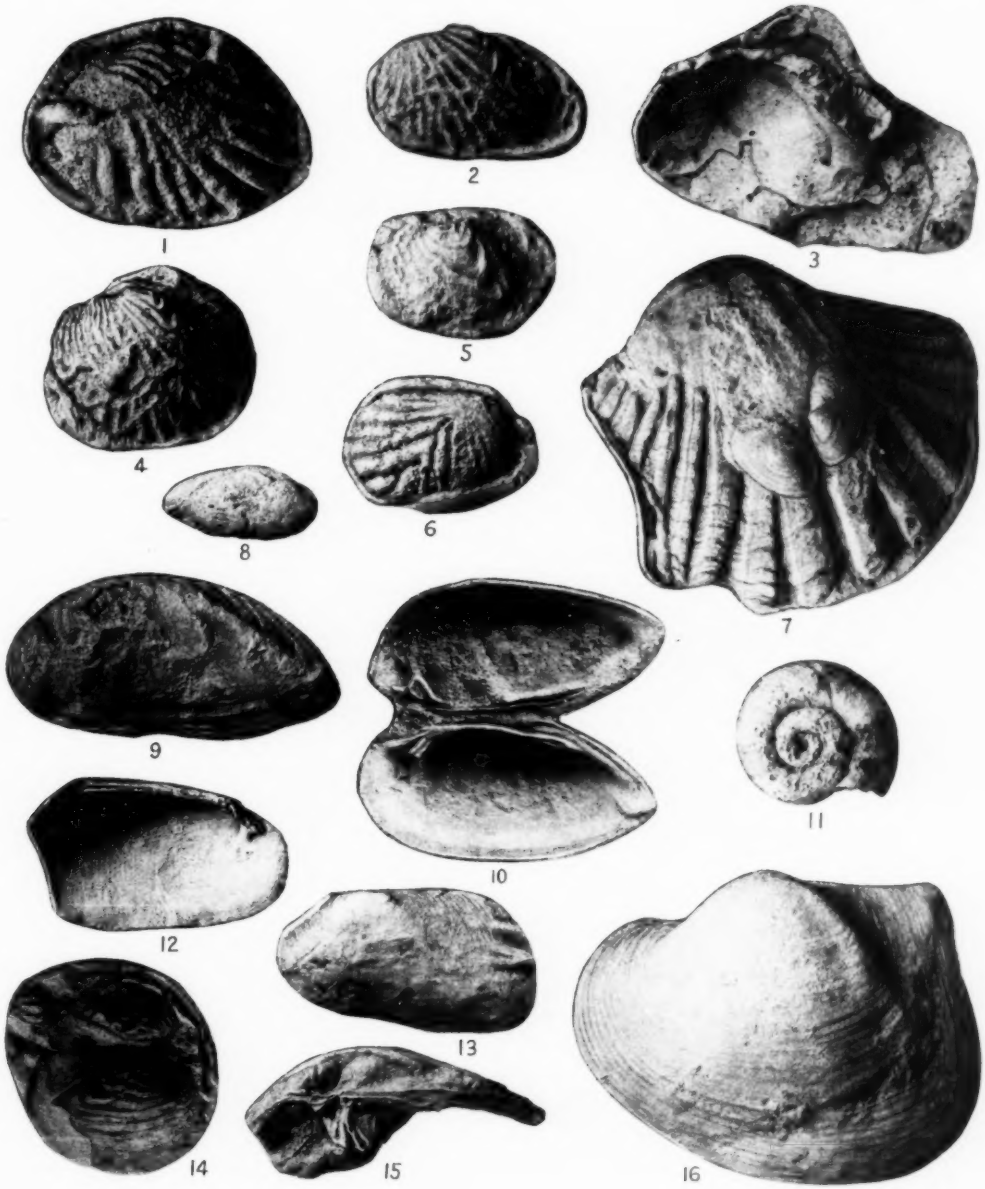
11—*Helisoma* sp., ×1½, U. S. N. M. cat. no. 372545. (p. 17)

12, 13—*Lampsilis bowlingi* MacNeil, n. sp., ×¾. 12, Interior of (left) valve; 13, exterior of same showing posterior fluting; holotype, U. S. N. M. cat. no. 372856. (p. 17)

14—(?) *Costanaia arciformis* MacNeil, n. sp., ×3, possibly a variation in the beak sculpture of this species. U. S. N. M. cat. no. 372543. (p. 13)

15—*Costanaia arciformis* MacNeil, n. sp., hinge of a medium-sized right valve. Paratype, U. S. N. M. cat. no. 371925. (p. 13)

16—*Lampsilis marshalli* MacNeil, n. sp., ×¾, posterior ventral portion restored. Holotype, U. S. N. M. cat. no. 372855. (p. 16)



MacNeil, Miocene mollusks

This species is named in honor of Mr. William B. Marshall, of the United States National Museum.

LAMPSILIS BOWLINGI MacNeil, n. sp.
Plate 5, figures 12, 13.

Shell obovate, higher posteriorly than anteriorly, posterior dorsal margin slightly winged; beaks low and at anterior quarter of shell; beak sculpture not known; concentric growth lines prominent; posterior slope marked off by a broadly rounded posterior rostrum; mid-posterior margin fluted by two or three short folds; pseudocardinal teeth of left valve two in number, arranged nearly linearly with an anteroventral inclination, the posterior one nearly in contact with and dorsally overlapping the anterior one; laterals double, long, and thin in left valve. Hinge of right valve unknown.

Holotype (U. S. N. M. cat. no. 372856), external and internal molds of a left valve measures: Length, 46 mm.; height, 23 ± mm.; convexity, 10 ± mm.

The posterior fluting is the unique feature of this species, and is seen in all three of the specimens at hand.

It is named in honor of Mr. Leslie Bowling, the collector of the material herein described.

Family SPHAERIIDAE Dall

Genus SPHAERIUM Scopoli

SPHAERIUM CF. S. RUGOSUM Meek

Sphaerium rugosum MEEK, *1870*, Acad. Nat. Sci. Philadelphia, Proc., App., p. 56.

Sphaerium rugosum MEEK, *1877*, U. S. Geol. Expl. 40th Par. vol. 4, p. 182, pl. 16, figs. 2, 2a, and 2b.

Sphaerium rugosum MEEK, WHITE, C. A., *1883*, U.S. Geol. Survey, 3d Ann. Rept. (1881–82), p. 440.

Several specimens of a fairly large *Sphaerium* show characters strongly suggestive of this Miocene species from Nevada. The suborbicular outline, nearly central beaks and stout laterals are the conspicuous features.

Dimensions: Length, 10 mm.; height, 7 mm.; convexity, 3 mm.

Genus MUSCULIUM Link

MUSCULIUM sp. ind.
Plate 5, figure 7

Two small valves resting on an eroded valve of *Costanaia arciformis* are probably referable to the genus *Musculium*, although their specific identity is uncertain.

Figured specimens: U. S. Nat. Mus. cat. no. 372547.

Dimensions: Length, 11 mm., height, 7 mm., convexity, 3 mm.

Genus HELISOMA Swainson

HELISOMA sp. ind.
Plate 5, figure 11

A single specimen of this genus was obtained and is the first gastropod to be recorded from the Catahoula sandstone.

Figured specimen: U. S. Nat. Mus. cat. no. 372545.

Dimensions: Diameter, 15 mm., thickness, 5 mm.

JOURNAL OF PALEONTOLOGY, VOL. 9, NO. 1, PP. 18–29, PLS. 6, 7, JANUARY, 1935

SYSTEMATIC POSITION OF THE STROMATOPOROIDEA[1]

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ABSTRACT

It is suggested that the Stromatoporoidea are related to the foraminiferal genus *Gypsina*, and are therefore best associated with the Foraminifera. This suggestion is based primarily on the similarity of the minute structure of certain species of *Actinostroma* to that of *Gypsina*. Accessory evidence is adduced from other genera of stromatoporoids, but it is believed that much more work is required to prove or disprove the suggestion offered.

The stromatoporoids, as reef builders and as horizon markers, play a part, more particularly in Silurian and Devonian time, that is not always fully appreciated. The difficulties of identification of species are in part responsible for the relatively slight interest in the group shown by most palaeontologists. The doubtful affinities of these organisms, and the consequently insecure basis of comparison and description have likewise contributed to their neglect. Species belonging to the order have been ascribed to the Algae, the Foraminifera, the Bryozoa, the Porifera, the Anthozoa, and the Hydrozoa. Since the appearance of Nicholson's monograph[2] the hydrozoan affinity has been generally accepted, not however without a growing feeling of dissatisfaction on the part of several investigators.

It is not my purpose to review the various opinions held, but to express my conviction that many species can best be referred to the Foraminifera, and that, by inference, the whole order, if it be a true taxonomic group, is to be so ascribed.

Dawson, in his defense of the organic nature of *Eozoön canadense*, considered the stromatoporoids to be Foraminifera and Lindström held the same opinion for at least the type genus *Stromatopora*.

I am indebted to Professor Sydney J. Hickson of Cambridge University for the suggestion of foraminiferal affinity and for specimens of modern sedentary Foraminifera for comparison. In a letter Professor Hickson states: "I feel very strongly that the palaeontologists ought to remove them all from the group of the Hydrozoa. There is really no evidence worth consideration that they were coelenterates. They may have differed from recent Foraminifera in some essential respects, but I feel they were rhizopodous Protozoa."[3]

[1] Manuscript received January 2, 1934.

[2] Nicholson, H. A., A monograph of the British stromatoporoids: *Palaeontogr. Soc., Mon.*, 1886–1892.

[3] Since this paper went to press Professor Hickson has published his views; On *Gypsina plana* and on the systematic position of the stromatoporoids: *Quart. Jour. Micros. Sci.*, vol. 76, pt. 3, January, 1934.

I have long doubted the hydrozoan relationship, but, having little knowledge of Foraminifera, that association did not appeal to me before I received the suggestion.

STRUCTURE OF *Gypsina Plana*

Gypsina plana Carter, is a sedentary species of the Foraminifera, of variable characteristics in different localities and under different conditions. It is world wide in distribution and ranges from shallows to 150 fathoms. From Professor Hickson I have specimens from the Red Sea and from Tahiti. A detailed account of the species is given by Miss Marjorie Lindsey.[3a] The test of the Red Sea specimen forms a thin encrustation on a coral; it is about a millimetre thick and the surface is smooth except that it conforms with the protuberances of the coral (Pl. 6, fig. 1). The test is made up of layers of minute chambers more or less regularly superimposed; in consequence, the outer walls of contiguous chambers are fairly coincident and build laminae. Where the chambers of one layer are superimposed on the chambers beneath there is a suggestion of tubular structure, and in vertical sections the impression of "pillars."

Vertical sections of the test show somewhat cyst-like chambers, in the lower part arranged in indefinite rows about 0.05 mm. apart; in the outer region the chambers are much flatter, oblong in shape, much closer together (7 in 0.16 mm.), and so definitely arranged in rows that the impression of laminae is pronounced. In this region, also, the superposition of chambers and vertical continuity of the lateral walls gives the appearance in vertical section that "pillars" would produce. Where the section traverses the plane of a lateral wall the foramina[4] can be seen, but not in the lateral or external walls of the chambers where cut across, probably because the section is thicker than the diameter of the foramina (Pl. 6, fig. 2).

Tangential sections show a distinct reticulation (lateral walls of the chambers). The fibre is about 0.02 mm. thick and the internal diameter of the mesh 0.04 to 0.06 mm. Where the plane of section lies in the external wall of a chamber, 12 to 16, or occasionally more, minute foramina may be seen. These pores are 0.005 mm. in diameter. It is to be noted that they can be seen in the mesh-work only where the section is extremely thin. (Pl. 6, figs. 3, 4).

The chambers have no inner wall or floor and the external wall is upwardly arched, more particularly in the lower levels of the test. The appearance of the vertical section is exactly like that of a fine-grained *Clathrodictyon*, with the "pillars" formed by downward inflections of the laminae. In places where the chambers are superimposed the "pillars" become continuous and, there-

[3a] Lindsey, Marjorie, On *Gypsina plana*, Carter, and the relations of the genus: *Linn. Soc. London, Trans.*, ser. 2, vol. 16, Zool., pp. 46–51, text figs. 1–6, 1913–1914.

[4] Foramen is here used for the pseudopodial pore; many authors use the term for the communication passage between chambers, the original meaning.

fore, the appearance of an *Actinostroma* is presented.

The tangential section with its reticulate structure does not suggest either typical *Clathrodictyon* or *Actinostroma* but it is exactly like that of certain species that have been ascribed to the latter genus. Herein lies the germ of the present paper.

COMPARISON OF *Gypsina plana* WITH SPECIES OF STROMATOPOROIDEA

Actinostroma tenuissimum Parks, has a test so like that of *Gypsina plana* that it can be distinguished only by its greater thickness and by its failure to reveal the minute foramina.[4a] This specimen is from the Niagara limestone, Scoharie county, New York. The test is about 10 mm. thick and is made up of minute chambers the internal diameter of which is about 0.04 mm. or less. The chambers are disposed in layers giving the impression of laminae, as viewed in vertical section. The imperfect laminae occur to the number of 5 or 6 in 0.16 mm. The walls of the chambers, where those structures are superimposed, give the appearance of pillars, about 5 in 0.16 mm. On this account the species was originally ascribed to *Actinostroma*. The tangential section, however, in the light of the hint given by *Gypsina*, is far better interpreted as a reticulation than as showing cut pillars connected by whorls of fibres. The meshes of the reticulation have an internal diameter of 0.04 mm. Four or five meshes occur in a distance of 0.16 mm. (Pl. 6, figs. 5, 6). Fine foramina for pseudopodia have not been observed.

The structure of *A. tenuissimum* is almost identical with that of *Gypsina plana*. The test is much thicker and the chambers slightly smaller. In view of the state of preservation it is not remarkable that the minute foramina for pesudopodia are not seen.

Other species ascribed to *Actinostroma* show the same structure. *A. whiteavesii* Nicholson, in tangential sections shows a distinct reticulation as in *Gypsina*.[5] The chambers are larger in this species and the "pillars" are more distinct. The tangential section shows a most distinct reticulation such as severed chambers would produce, and not a trace of cut pillars or of whorls of fibres so char-

[4a] Parks, W. A., Silurian stromatoporoids of America: *Univ. Toronto Stud. Geol. Ser.*, no. 6, p. 42, pl. 18, figs. 2, 3, 9, 12, 1909.

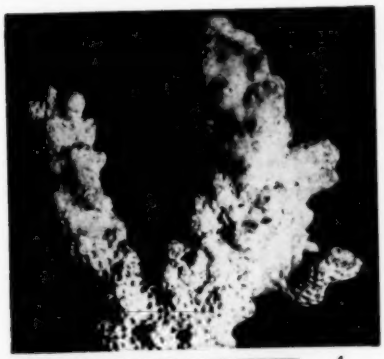
[5] Nicholson, H. A., On some new or imperfectly known species of stromatoporoids: *Ann. Mag. Nat. Hist.*, p. 320, pl. 9, figs. 3, 4, April, 1891.

EXPLANATION OF PLATE 6

FIGS. 1–4—*Gypsina plana* Carter. 1, Nat. size, Red Sea; 2, vertical section, ×25, Red Sea; 3, tangential section, ×25, Red Sea; 4, tangential section, ×25, Tahiti. (p. 19)

5–7—*Actinostroma tenuissimum* Parks, Niagara limestone, Schoharie County, New York. 5, Vertical section, ×25; 6, tangential section, ×25; the reticular structure is masked by refracting lines; a portion in the upper right corner has been accentuated in ink; 7, tangential section, ×10; the reticular structure is well shown by this magnification. (p. 20)

8—*Actinostroma perforatum* Parks, Silurian, Gaspé, Canada. Tangential section, ×25; note the general reticulate structure and the small pores in the fibre. (p. 27)



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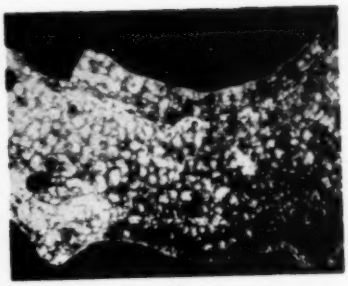

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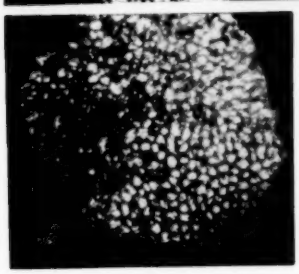

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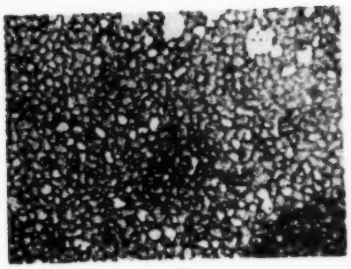

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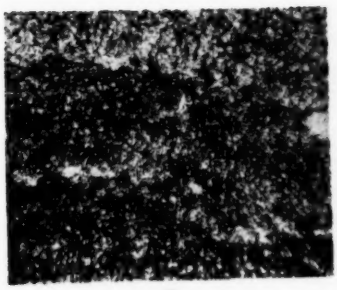

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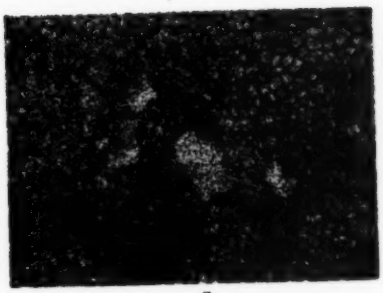

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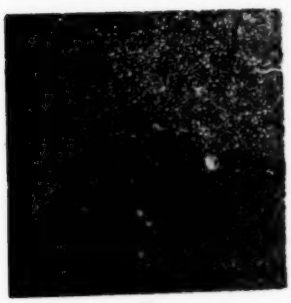

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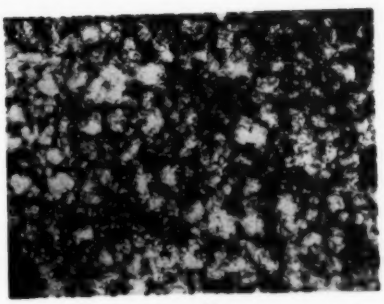


8

Parks, Stromatoporoidea

acteristic of true *Actinostroma*. Further, the "pillars" in vertical section are zig-zag lines representing the more or less continuous, somewhat curved lateral walls of the superimposed chambers. In this case the chambers are much larger than in *A. tenuissimum* being about 0.2 mm. in internal diameter (*op. cit.*, Pl. 9, fig. 3).

Actinostroma mirum Parks, is a remarkable species from the Silurian of Chaleur Bay.[6] The size and shape of the test is unknown but it is at least 20 mm. thick. The fibre consists of layers of vesicles (chambers) more strictly in rows than in *A. tenuissimum;* in consequence, the "laminae" seem to be better defined. On the other hand, the superposition of chambers is less pronounced and the *Actinostroma*-like pillars are seen in only a few places in vertical section. In fact, the structure is as much *Clathrodictyon*-like as *Actinostroma*-like. The tangential section shows a distinct reticulation as in *Gypsina*. It is true, also, that a suggestion of whorls of fibres is to be observed in places. The outer walls of the chambers (laminae) are 0.04 to 0.05 mm. apart. The fibre in tangential section is about 0.015 mm. thick and the internal diameter of the mesh is about 0.04 mm. This species, in the structure of its fibre and the size of the chambers, is very like *Gypsina* and *A. tenuissimum* but the laminae are more pronounced and the pillars less so than in the latter species (Pl. 7, figs. 1, 2).

On the similarity of skeletal structure alone these species of *Actinostroma* closely resemble *Gypsina*—far more closely than they approach either *Millepora* or *Hydractinia*.

Actinostroma mirum shows another feature of great significance. The skeletal fibre as described above is pierced vertically by "pores" about 0.16 mm. in diameter and about 0.32 mm. from centre to centre. These pores have no walls and are crossed at varying intervals (0.08 mm.) by strands of the fibre. They are exactly like the so-called zooidal pores of the milleporoid stromatoporoids. According to the present interpretation, they represent a series of larger chambers strictly superimposed. Are they special chambers for the protrusion of pseudopodia? Whatever their function may be they are not zooidal, and, by inference, neither are the analogous pores in milleporoid stromatoporoids zooidal.

STRUCTURE OF STROMATOPORIDAE

Nature of fibre.—The argument for the foraminiferal affinities is based primarily on the striking resemblance to *Gypsina* of the three species described above and which, eventually, together with other species must be removed to a new genus. The fibre of *A. mirum* is so like that of *A. tenuissimum* that the two cannot be separated generically. *A. mirum*, however, has the conspicuous vertical pores and at once suggests *Stromatopora*. A question naturally arises as to the nature of the spongy fibre of

[6] Parks, W. A., New species of stromatoporoids, sponges, and corals from the Silurian strata of Baie des Chaleurs: *Univ. Toronto Stud. Geol. Ser.*, no. 33, p. 6, Pl. 1, figs. 5, 6, 1933.

Stromatopora. In many species it is certainly true that the fibre is nothing but a mass of inosculating strands without orientation. It is just as true, however, that species occur in which orientation does exist and the fibre is made up of vertical and horizontal elements, thus resembling that of the species described above. Tissue of this kind is seen in *Stromatopora constellata* Hall, *S. foveolata* Girty, *S. corallifera* Hall & Whitfield, *Syringostroma centrotum* Girty, *S. barretti* Girty, *Stromatopora compacta* Parks, and many other species. Further, the size of the mesh is comparable with that seen in *Actinostroma tenuissimum* or *Gypsina plana* and the transverse section is a reticulation. A distinctly reticulate fibre is seen also in numerous species of *Stromatoporella*. *S. granulata* Nicholson, from the Hamilton formation of Ontario, is an excellent example. In this species the "laminae" are composed typically of a single layer of minute *chambers*, 0.03 mm. from centre to centre. As seen in vertical section these chambers are distinctly closed above and below and are not in the nature of pores through the lamina. In cross section a distinct and regular reticulation is seen (Pl. 7, figs. 3, 4).

It may be stated, therefore, that in many genera and species of the family Stromatoporidae the ultimate fibre is composed of chambers not differing greatly from those of *Actinostroma tenuissimum* or of the modern *Gypsina*. With regard to those species in which the fibre is truly "spongy," it may be inferred that the regular chambers have deteriorated to a mass of irregular cysts.

Vertical pores and astrorhizae.—Two general types of vacuities occur in the test of Stromatoporidae—vertical pores (the so-called zooidal pores), and the horizontal canals of the astrorhizal systems. The vertical pores are heralded in *Actinostroma mirum*. They may be interpreted as representing the "apertures" of Foraminifera for the protrusion of pseudopodia, as special cells for the same purpose, or as interskeletal canals for the circulation of the protoplasm. Doubtless the same function may be ascribed to them in *Stromatopora*. The horizontal astrorhizal canals always communicate directly with the vertical pores when both are present. May we ascribe to the astrorhizae the same function? I can suggest no other explanations, but must admit many objections. The astrorhizal canals are not confined to a single layer of chambers but to a fairly constant yet limited number in any given species thus defining the laminae (old sense). The astrorhizal centres may, or may not, be superimposed, but they are usually equidistant. Now, if the analogy with *Gypsina* is to be maintained, we must assume that each layer of minute chambers advanced laterally over the preceding layer in the growth of the test. How then, could the position of astrorhizal centres be determined? If we assume that each layer of chambers extended outward from the astrorhizal centres, how were those centres fixed in the first layer of chambers? The needs of the organism doubtless determined the position

and strength of the astrorhizal systems and it is to be remembered that they are absent in many species. Careful examination of young tests might yield information as to the origin of both astrorhizal and vertical pores. In *Gypsina* there are no connections between chambers other than the foramina and the same condition seems to maintain in the forms under review. The vertical pores and the astrorhizae can scarcely be interpreted as avenues of communication between chambers, as they are in relation to relatively few of the myriads of chambers in the test. In many modern Foraminifera the protoplasm is without as well as within the test. The growth of the test of stromatoporoids may have been greatly influenced by this disposition of the protoplasm. Information as to the manner in which new chambers appear in *Gypsina* would be of value.

COMPARISON WITH TYPICAL "HYDRACTINOIDS"

The argument thus far applies only to the so-called milleporoid stromatoporoids and to certain fine-grained types ascribed, perhaps erroneously, to *Actinostroma*. The extension of the analogy with *Gypsina* to the hydractinoid group is largely conjectural but it is not entirely unsupported by evidence.

If we admit that the species of *Actinostroma* referred to are really Foraminifera, then the small cavities must represent the interiors of chambers. The question naturally follows —Do the interspaces in typical and often much coarser species of *Clathrodictyon* and *Actinostroma* represent chambers? At first sight this conclusion seems reasonable. There is, however, a second interpretation in which the interspaces are regarded as mere interstices and which, on the whole, appeals to me more strongly.

Under the hypothesis that the interspaces represent chambers, the derivation of typical species of *Actinostroma* and *Clathrodictyon* from the reticulate type allied to *Gypsina* may have been as follows:

First hypothesis.—Typical *Actinostroma* is described as consisting of true continuous pillars which give off whorls of fibres at intervals, thus forming the laminae. The pillars are undoubted, but the whorls of fibres are seen only in certain species; I doubt the inference that the laminae are formed in this manner in all species of the genus. It may be assumed that true *Actinostroma* arises from a stock in which the chambers are strictly superimposed, by the breaking down of the lateral walls of the chambers and the concentration of the tissue at the confluent angles. Similarly, in the most typical cases, the outer wall breaks down to the "whorl of fibres." The only evidence in support of this assumption is afforded by *Actinostroma astroites* (Von Rosen), originally described from the Silurian of Esthonia. The vertical section of this species, in fineness of grain and in the general nature of the fibre, can scarcely be distinguished from that of *A. tenuissimum*. The tangential section, however, is distinctly different, showing no regular reticulation as in *A. tenuissimum*

and in *Gypsina*, but dots representing the cut pillars. In the plane of a lamina the dots are connected by whorls of fibres. The similarity of the vertical sections suggest affinity and the above assumption would account for the differences. The extension of the analogy to all known species of *Actinostroma* requires no further assumption.

The test in the genus *Clathrodictyon* may be regarded as composed of layers of chambers in which superposition does not occur and in which the lateral walls break down into pillars at the angles of junction. Under the present assumption, the test of the genotype, *C. vesiculosum*, is distinctly made up of irregular layers of cysts (chambers) one above the other without any direct superposition of chambers. The cysts, however, are imperfect laterally, communicating with one another through openings so large that the lateral walls are reduced to imperfect sinuous plates or even to pillars. The outer walls, however, remain intact and those of contiguous chambers unite to form continuous, if crumpled and irregular, "laminae." The "pillars" can scarcely be called structures as they are merely the remnants of lateral walls. In other species, the lateral communication is so extensive that the pillars appear as sharp downward (and upward to a less extent) inflections of the laminae. Finally, there are many species in which the laminae are even and distinct, and the pillars definite connecting structure holding the laminae together.

Nicholson held that in *Actinostroma* the pillars are the primary structures and that the laminae are formed by whorls of fibres from the pillars. He extends this interpretation to *Clathrodictyon*, but I am aware of no observation in support of this view. The pillars of *Clathrodictyon* undoubtedly arise from the laminae. The present suggestion is, that in both genera, the pillars are residua of the lateral walls of chambers, situated at the angles of junction.

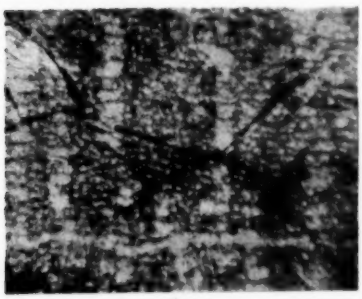
EXPLANATION OF PLATE 7

FIGS. 1, 2—*Actinostromum mirum* Parks, Silurian, Chaleur Bay, Canada. 1, Vertical section, ×25; shows horizontal rows of small chambers and large vertical openings; 2, tangential section, ×25; shows the reticulate fibre (chambers) and the large vertical pores. (p. 21)

3, 4—*Stromatoporella granulata* Nicholson, Hamilton formation, Ontario. 3, Vertical section, ×25; the laminae are composed of chambers; the pillars are inflections of the laminae; 4, tangential section, ×25; shows the reticulate structure of the lamina; the large openings are the hollows of inflected points (pillars). (p. 22)

5, 6—*Clathrodictyon problematicum* Parks, of Onondaga age. 5, Vertical section, ×25; the lower lamina shows the cellular or chambered structure; the oval in the center is an obliquely cut *Caunopora* tube; 6, tangential section, ×25; the chambered structure of a lamina is shown in the middle of the figure; the severed pillars are dense. (p. 25)

7, 8—*Clathrodictyon* (?) *n. sp.*, Hamilton formation, Michigan. 7, Vertical section, ×25; note the coarsely chambered laminae and the dense pillars; 8, tangential section, ×25; shows the chambers of a lamina; chambers are much larger than in *Gypsina*. (p. 26)



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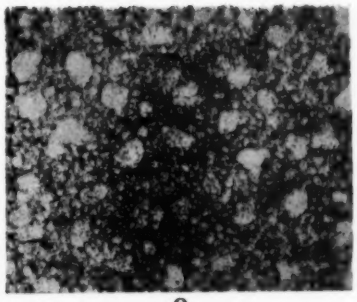

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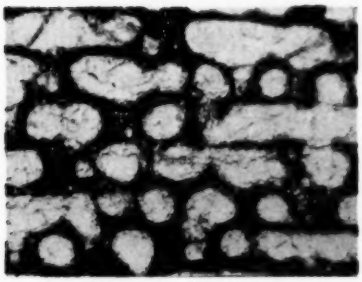

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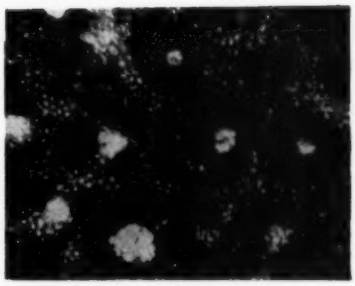

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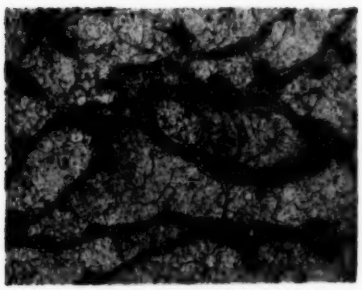

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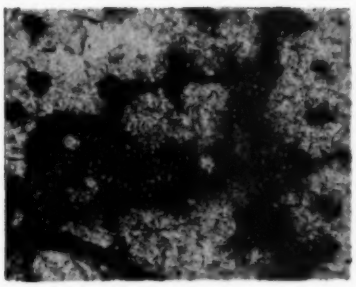

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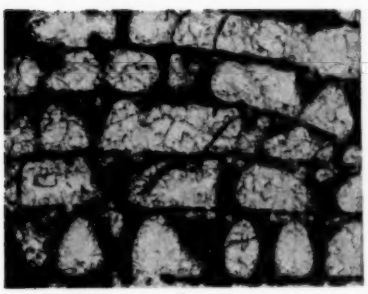

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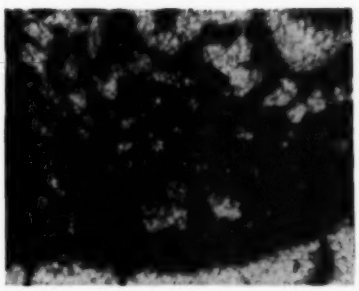

8

Parks, Stromatoporoidea

In *Actinostroma* the chambers are superimposed and, therefore, the pillars are continuous. In *Clathrodictyon* the chambers are not superimposed and, consequently, the pillars reach only from lamina to lamina. Further, in the most typical *Actinostroma* the outer walls of the chambers have broken down into "whorls of fibres"; in *Clathrodictyon* the outer walls of the chambers remain firm and have a greater tendency to unite into distinct continuous laminae.

In nearly all species of *Clathrodictyon* the outer wall (lamina) seems to be quite imperforate, but in view of the state of preservation and the minute size of the openings, it is impossible to make the definite statement that pores are absent. In *Gypsina* there is no communication between chambers except by the pores.

Second hypothesis.—The second assumption, *i.e.*, that the interspaces of *Clathrodictyon*, of *Actinostroma*, and of some species of *Stromatoporella* are to be regarded as mere interstices has considerable evidence in its favor.

While nearly all the species ascribed to *Clathrodictyon* have imperforate walls, two at least, *C. cellulosum* Nicholson and *C. problematicum* Parks, are described as having perforate walls. There is a remarkable resemblance, in the structure of the laminae of these two species, to that of certain species of *Stromatoporella*. Vertical sections, also, of these species of *Stromatoporella* can not be distinguished from similar sections of typical species of *Clathrodictyon* except by an examination of the intimate structure of the fibre.

In *Clathrodictyon cellulosum*, *C. problematicum*, and several species of *Stromatoporella* the laminae seem to be pierced by pores. Examined closely, in vertical section, however, the pores appear to be evenly spaced and closed above and below. Tangential sections of the laminae show a distinct reticulation quite analogous to that of *Gypsina*. In *Clathrodictyon problematicum* the pores are 0.015 mm. in diameter and 0.04 mm. from centre to centre (Pl. 7, figs. 5, 6). These openings are either distinct pores or they represent foraminiferal chambers; the latter view is suggested by their large size, the closing above and below, and their strong resemblance to the chambers of *Gypsina* and to those of the species of *Actinostroma*, on which the argument for foraminiferal affinity is based. The laminae of these two species may be regarded, therefore, as sheets composed of a single layer of chambers. The pillars arise as inflections of the laminae and the interspaces are mere interstices.

Essentially the same structure occurs in several species ascribed (perhaps erroneously) to *Stromatoporella*. *S. granulata* and *S. mammillata* are good examples. Examined under low magnification these species can scarcely be distinguished from *Clathrodictyon*, but under higher magnification, they show the "spongy" fibre of the "milleporoid" group. On this account and because in cross section they show ring-like sections, regarded as concentrations of the fibre around zooidal pores, they were ascribed to *Stromatoporella*. I have no hesitation

in saying that both these observations have been wrongly interpreted. The "spongy" fibre is not spongy; in tangential section it is a distinct reticulation (Pl. 7, fig. 4) and the meshes are not greatly different in size from those of *Gypsina*. In vertical section the tissue of the laminae and of the pillars is evidently composed of little cells which, under the present assumption, are interpreted as chambers precisely as in *Clathrodictyon cellulosum* and *C. problematicum* (Pl. 7, fig. 4). The "pillars" are pointed inflections of the laminae and thus appear as rings in cross section, as also in the two species of *Clathrodictyon*. While not pertinent to the present argument, it is obvious that these species of *Clathrodictyon* and of *Stromatoporella* must be grouped together as a new genus. We have, therefore, in this new genus either: (*a*) forms related to *Clathrodictyon*, but with large pores in the walls, or (*b*) sheets composed usually of a single layer of chambers, these sheets bent into sharp inflections (pillars) to connect with the layer adjoining. It is necessary, under this assumption to account for the interlaminar spaces—the open space around and between the pillars. Under the "milleporoid" hypothesis these spaces must represent horizontal astrorhizal canals but there are no astrorhizae to be seen on excellently preserved specimens showing the surface. The assumption is untenable, as also is the theory of short zooidal pores. We must suppose, therefore, that in this group the new chambers extended in a sheet-like manner, not in contact with the layer below but sending down points at intervals to make connection. This explanation is very attractive; unfortunately, however, it is difficult to extend it to the ordinary species of *Clathrodictyon* and *Actinostroma* in which the fibre is dense.

I have before me, however, an interesting intermediate type from the Hamilton formation of Michigan. The species will be described as new in a forthcoming publication, but I am as yet uncertain whether to ascribe it to *Clathrodictyon* or to *Stromatoporella* or to the new genus (Pl. 7, figs. 7, 8). In this form the general appearance is that of a *Clathrodictyon* The pillars are quite dense but their origin as downwardly inflected points of the laminae is obvious. The laminae, however, present a cellular structure similar to but coarser than that seen in the species of *Stromatoporella* cited above. Under the old conception the species is "milleporoid" in the laminae, and "hydractinoid" in the pillars. Under the present conception the test consists of sheets of small chambers connected by dense pillars that are largely but not entirely independent of the laminae. This form is from the Hamilton formation and is contemporaneous with *Stromatoporella granulata* but later than *S. mammillata* and *Clathrodictyon problematicum* (of Onondaga age). It seems to prove that dense pillars may arise by modification of inflected points of chambered laminae. One might conclude that a similar loss of chambers in the laminae would produce a *Clathrodictyon*

or an *Actinostroma* but it is impossible to make this assumption because the typical species of *Clathrodictyon* and *Actinostroma* are chiefly Silurian and, therefore, earlier than these exceptional types.

It would appear, therefore, that we must look for an explanation by which a typical *Clathrodictyon* might pass into *C. cellulosum* and into the species of *Stromatoporella* cited above. In considering this question one must be allowed a wide latitude of supposition, and any suggestions offered must be regarded as tentative only. In *C. cellulosum* and *C. problematicum* we have typical *Clathrodictyon* except for the fact that the laminae seem to be made up of little cells instead of being structureless. As these forms are of Middle Devonian age and as most species of the genus are Silurian, the chambered structure would seem to be a later characteristic. Is it too speculative to suggest that the early forms of the genus had chitinous chambers and secreted only a basal layer of carbonate of lime? Under this suggestion the familiar laminae of *Clathrodictyon* consist of the confluent floors of small hypothetical chambers and the interlaminar spaces are mere interstices and do not represent chambers as under the first supposition. The "pillars" are merely connecting processes, either inflections of the laminae or definite structures. The suggestion is attractive because it allows us to bring Ordovician genera like *Stromatocerium* and *Beatricea* into the same category. This conception of the nature of *Clathrodictyon* is, of course, different from that of the first hypothesis. Further, in view of the general similarity of *Actinostroma* and *Clathrodictyon*, the acceptance of the present hypothesis of the origin of *Clathrodictyon* demands that it be extended to *Actinostroma*. It is impossible to regard the interspaces as interstices in *Clathrodictyon* and as chambers in *Actinostroma*. In *A. tenuissimum* and *A. mirum* the interspaces do represent chambers. The whole of the argument for foraminiferal affinity is based on this assumption. It is not impossible, however, to regard these fine-grained, reticulate species of *Actinostroma* as a group by themselves—the antecedents of the "milleporoid" stromatoporoids—and for the coarser, more typical species of *Actinostroma* to assume an origin similar to that of *Clathrodictyon*, *i. e.*, chambered sheets with pointed inflections at intervals and these inflections superimposed to form the continuous pillars.

The only evidence in support of this view is given by *Actinostroma perforatum* Parks, and this evidence is far from convincing. This peculiar species is from the Silurian of Gaspé. The vertical section shows typical *Actinostroma* pillars connected by very irregular horizontal elements. The tangential section, however, is strikingly different from that of any other stromatoporoid that I have examined. Cut pillars are not distinctly seen but there appears to be a sort of irregular mesh about 0.2 mm. in diameter. The fibre of the mesh, in part at least, as well as that of other bands crossing the meshes

shows distinct perforations about 0.02 mm. in diameter (Pl. 6, fig. 8). Are these perforations pores in the walls of large chambers or do they represent chambers themselves? The large size of the openings and the fact that pseudopodial foramina have never been observed in a stromatoporoid incline one to favor the latter view. In *Gypsina plana*, regarded as coarse-pored, the foramina are only 0.005 mm. in diameter. Accepting this view, we have in this species an *Actinostroma* composed of chambered sheets sending down dense pillars at intervals and thus bringing *Actinostroma* into the same category as *Clathrodictyon* under our second hypothesis.

SUMMARY OF EVIDENCE BASED ON FIBRE

Summing up the evidence thus far we have the following observations, deductions, and inferences in favor of the foraminiferal nature of stromatoporoids.

(1) The structure of certain species of *Actinostroma* is very near that of the modern *Gypsina*.
(2) Reticulate or cellular fibre rather than mere spongy fibre occurs in species of *Stromatopora*.
(3) Vertical pores occur in *Actinostroma mirum;* in consequence, they cannot be "zooidal."
(4) Certain species of *Stromatoporella* strongly suggest laminae made of a single layer of chambers, not residual spongy fibre.
(5) This type of *Stromatoporella* is not separable from *Clathrodictyon cellulosum* and *C. problematicum* and all of them have the gross structure of typical *Clathrodictyon*.
(6) Typical *Clathrodictyon* and *Actinostroma* may be regarded in different ways:
    (a) As derived from the chambered type like *A. mirum*. The pillars are contractions of the lateral walls of the chambers. The interlaminar spaces are confluent chambers.
    (b) The laminae are composed of chambers of which only the floors were made (or are preserved). The interlaminar spaces are interstices, and the pillars primarily inflections of the laminae, superimposed in *Actinostroma*, irregular in *Clathrodictyon*.

BASAL CHAMBERS

Another argument in favor of the foraminiferal association is the occurrence in many stromatoporoids of a basal layer of chambers quite different from those of the general test. In some species this layer occurs at the base of each latilamina. It is possible that these basal chambers represent the proloculum, megalospheric or microspheric, of normal Foraminifera.

CAUNOPORA TUBES

The occurrence of *Caunopora* tubes has long been an unexplained phenomenon. These tubes, of relatively large size, traverse the test of many stromatoporoids but they may or may not be present in different specimens of the same species. I have convinced myself by the examination of numerous examples that *Caunopora* tubes belong to the organism and that they are not included corals as has been suggested. If we accept the foraminiferal nature of the order, a

plausible explanation is afforded. In many recent and fossil Foraminifera there is a distinct alternation of generations; it is probable, also, that this distinction applies to all species. The so-called microspheric stage gives rise asexually to a new organism, the megalospheric stage, which reproduces sexually. In the stromatoporoids, therefore, the tests with *Caunopora* tubes may be regarded as representing one of the alternate generations, probably the megalospheric or sexual stage.

SUMMARY

Many of the statements made in this paper are in the nature of suggestions or possible explanations without adequate proof. Much more work is required to prove or disprove the suggestions offered. There are, nevertheless, certain observed facts that must be accepted whatever deductions may be drawn from them:

(1) The fibre of some species of stromatoporoids is nearer to that of the modern foraminifer *Gypsina* than to that of any hydrozoan.
(2) *Actinostroma mirum* shows vertical tubes exactly like those of the "milleporoid" Stromatoporidae.
(3) The interlaminar spaces of certain species of *Stromatoporella* are not due to horizontal canals of astrorhizal systems but are quite analogous to the interlaminar spaces in *Clathrodictyon*.
(4) Forms like *Clathrodictyon problematicum* and *C. cellulosum* indicate clearly the passage of *Clathrodictyon* into the species of *Stromatoporella* mentioned above.

It is fairly certain, also, that *Actinostroma mirum* shows a transition between the "hydractinoid" and the "milleporoid" divisions of Nicholson and justifies the conclusion that these divisions are not of taxonomic value. This conclusion is supported by the fact that certain species of *Clathrodictyon* pass into species (perhaps erroneously) ascribed to *Stromatoporella*.

SUGGESTED DEVELOPMENT

The following development history is suggested. It is highly conjectural and involves two hypotheses at variance with each other. It may, however, serve as a basis for further discussion.

(1) The original stromatoporoid was a laminar expansion of a single layer of chitinous chambers.
(2) By calcification of the walls and superposition of the layers arose types like *A. tenuissimum* and thence the Recent *Gypsina*.
(3) True Stromatoporidae arose by the loss of orientation of the chamber walls of (2).
(4) *Clathrodictyon* (and possibly *Beatricea*) arose from (2) by calcification of the floors of the chambers only, and by the laminae thus formed not being directly superimposed but being connected to one another by inflections, thus leaving interspaces. Typical *Actinostroma* might be derived by the regular superposition of the inflections, or
(5) Typical *Actinostroma* and *Clathrodictyon* may both be derived from types like (2) by the lateral walls of the chambers being concentrated into pillars at the angles of junction.
(6) Certain types of *Stromatoporella* arose from *Clathrodictyon* by the development of calcified chambers, or
(7) By the development of pores in the outer walls of chambers as under (5).

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TWO ANTHRACOLITHIC CORALS FROM BRITISH COLUMBIA AND RELATED SPECIES FROM THE TETHYS[1]

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ABSTRACT

This paper describes a new species of *Waagenophyllum* Hayasaka, 1924, and a species of *Caninia* Michelin, 1840, both from Keremos, British Columbia, and probably of Permian age. The genus *Waagenophyllum* is diagnosed and discussed and a few species from the Tethys are redescribed. The occurrence of other Tethyan fossils in western Canada is briefly reviewed. Bibliography.

This paper is concerned with a small lot of corals collected by Dr. H. S. Bostock, of the Geological Survey of Canada, in the Similkameen district, British Columbia. These corals are from a limestone outcrop on the south side of the ridge between Blind and Barslow Creeks, four miles east of Keremeos, a town about 150 miles east of Vancouver. The limestone is cut off by faults on all sides except the north, where it is unconformably overlain by Tertiary (Eocene?) volcanic rocks. The stone embedding the coral is black, crinoidal, slightly silicified and much fractured by small cracks. No organisms except encrinite ossicles and corals were found in the sections cut.

Dr. E. M. Kindle, who transmitted this material for study was not quite certain as to the age of the limestone, but considered it to be either Permian or Triassic.

The corals, which include a new form of *Waagenophyllum* Hayasaka and an unnameable species of *Caninia* Michelin, point very definitely to a late Palaeozoic age and show unmistakable affinity with the Anthracolithic corals of the Tethys.

The *Caninia*, it is true, does not help much in deciding the age of the bed except in indicating that it is Palaeozoic and not Mesozoic, the genus having a wide time range and a wide geographical distribution.

The *Waagenophyllum*, on the other hand, affords very clear evidence of an Upper Carboniferous or (more probably) Permian age and a Tethyan facies. The genus belongs to the Lonsdaleidae—a family of corals highly characteristic of the Permian of the Tethys. The genotype, *W. indicum* (Waagen & Wentzel), redescribed here, is a late Permian form distributed through the Tethys and ranging from China to West Serbia.

Within recent years a number of other species of *Waagenophyllum* have been described from the Anthracolithic limestones of Asia. Of these *Waagenophyllum columbicum*, n. sp., most closely resembles perhaps the Uralian form from the Himalayas described on p. 38.

[1] Manuscript received July 3, 1934.

As far as I am aware, the Canadian coral is the first of this important group to be recorded from North America,[2] although the existence of an Anthracolithic fauna both in West Canada and also in the southwestern United States is well established.

Permian fossils with Asiatic affinities have been described from three widely separated localities in British Columbia. E. M. Kindle, 1926, published an interesting list of Permian fossils from French Mountain in the Cassiar district, some 800 miles north of Keremeos. These were chiefly brachiopods, and among them was a *Leptodus*[3] which Kindle places near *Leptodus tenuis* (Waagen), from the *Productus* Limestone of the Salt Range. *Leptodus* is one of the most characteristic fossils of the Tethyan Permian. Kindle considers the Cassiar fauna to be allied to that of the Middle *Productus* Limestone (the Khund Ghat Beds) of India. C. O. Dunbar (1932) redescribed as *Neoschwagerina columbiana* a fusulinid which Dawson (1879, p. 74) had previously described as *Loftusia columbiana*, from the neighbourhood of Lillooet, on the Frazer River, 120 miles northwest of Keremeos. Dunbar considers the Canadian *Neoschwagerina* to be very similar to the oriental species *N. margaritae* (Deprat, 1913, p. 58, pl. 8, fig. 10 and pl. 9, figs. 1–3) and *N. craticulifera* (=*Schwagerina craticulifera* Schwager, 1883, p. 140, pl. 18, figs. 15–25), and thinks it may be even identical with the former. Arguing on the absence from the slide of certain types of Foraminifera, he infers a Lower or Middle rather than Upper Permian age for the specimen. Dunbar remarks that the only other record of the genus from North America is that of *Neoschwagerina* sp. ind. from California (Staff, 1912, p. 161). Later in the same year M. A. Fritz described 17 species of Permian Bryozoa from Strathcona Park, Vancouver Island, 350 miles west of Keremeos. The assemblage bears a resemblance to that from the Island of Timor in the East Indies described by R. S. Bassler (1929). Ten of the Canadian species are new, but four are common to Vancouver Island and Timor and three are identified with forms described by Waagen and his associates from the Salt Range.

Of late Palaeozoic faunas with Tethyan relationships recorded from the United States, mention need only be made here of the important Permian assemblage from the Guadaloupe Mountains, New Mexico, made

[2] In the Sedgwick Museum, Cambridge, a *Lonsdaleia* from Colombia, South America, to be described shortly by Dr. H. Dighton Thomas, has certain waagenophylloid characters. The Colombian fauna is Upper Carboniferous and very similar to the Uralian fauna of the Amazon, Peru, and Bolivia. (Derby, 1874, 1894; Meyer, 1914; Kozlowski, 1914.)

There are in the British Museum several specimens of a typical *Lonsdaleia* from "Berg Island, Arctic America." These, however, are identical with the Lower Carboniferous species *L. duplicata* (Martin), characteristic of Northern Europe. These fossils have been in the Museum from a very early date and the museum has no information.

[3] The name "*Leptodus*," given to the aberrant brachiopod by Kayser (1883, p. 161), has priority, although a very slight one, over "*Lyttonia*," proposed for the same fossil by Waagen (1883, p. 396), the name more generally although unwarrantedly used. The fact that Kayser gave the name to the fossil under a misapprehension does not in any way invalidate it.

known by Girty (1908), and that from the Glass Mountains, western Texas, described by Böse (1917) and King (1930), and of the Pennsylvanian fauna from North Central Texas described by Plummer and Moore (1921). Few corals, however, have been recorded from these formations. Plummer and Moore mention some from the Pennsylvanian, but none of them suggests any special affinities with the Tethyan species, whilst Girty (1908, p. 13) remarks concerning the faunal assemblage of the Guadaloupe Mountains:

> Coelenterates are more rare, small, and poorly differentiated. The absence of forms like *Lonsdaleia*, *Michelinia*, and the stromatoporoids, such as are found in some of the Asiatic faunas, is worthy of note, as is also the presence of *Cladopora*, which is a rather characteristic fossil of some of the lower beds. On the whole, however, the coelenterate fauna is rather meager and colorless.

The occurrence of Anthracolithic rocks in two widely separated regions in western North America—Keremeos, which is the most southern of the Canadian localities, is about 1400 miles N.N.W. of the Texas and New Mexico areas—suggests the possibility of two separate embayments. British Columbia, it is interesting to notes, lies much further north than any of the Asiatic regions in which Tethyan deposits of the same age have been recognised. Dunbar (1932, p. 48) suggests that the route taken by the oriental faunas was around the northern margin of the Pacific and that they entered the Cordilleran through from the north.

DESCRIPTION OF SPECIES

Genus WAAGENOPHYLLUM Hayasaka, 1924

The name *Waagenophyllum* was proposed by Hayasaka (1924, p. 23) in place of *Waagenella* Yabe and Hayasaka (1915, p. 96), which is preoccupied by De Koninck (1883, explanation of Pl. 38) for a Lower Carboniferous gasteropod, not by Gemmellaro (1889, p. 176; and (1890, p. 116), as stated by Hayasaka. De Koninck, it may be added, substituted *Waagenella* for *Waagenia* De Koninck (1883, p. 145), preoccupied by *Waagenia* Neumayr (1878, p. 60), a Jurassic ammonite.

Genosyntypes.—Lonsdaleia rugosa McCoy, 1849, p. 13. 1851, p. 105, pl. 3 B , figs. 6, 6a–c. Viséan, *Dibunophyllum* zone. Corwen. North Wales.

Lonsdaleia indica Waagen and Wentzel, 1886, p. 897, pl. 101, figs. 1–3; pl. 115, figs. 3, 4. Permian. Middle and Upper *Productus* Limestone. Various localities. Salt Range.

Lonsdaleia virgalensis Waagen and Wentzel, 1886, p. 900, pl. 101, fig. 4; pl. 116, fig. 2. Permian, Middle *Productus* Limestone. Virgal, Salt Range.

Lonsdaleia salinaria Waagen and Wentzel, 1886, p. 895, pl. 100, figs. 1, 3, 4. Permian, Middle *Productus* Limestone. Virgal, Vurcha, Musakheyl, Omarkheyl.

Lonsdaleia Wynnei Waagen and Wentzel, 1886, p. 896, pl. 99, fig. 2; pl. 100, figs. 5, 6. Permian, Middle *Productus* limestone. Katta.

Lonsdaleia akasakensis Yabe, 1902, p. 4, text-fig. 3. Permian, *Neoschwagerina globosa* limestone. Kinshôzan, Akasaka, Province Mino, Japan.

Lithostrotion jourdyi Mansuy, 1912, p. 69, p. 13, fig. 5. Carboniferous, Si-lu-lao, Tonkin, China.

Lithostrotion mixtum Mansuy, 1912, pl. 38, pl. 8 fig. 5. Carboniferous, horizon undetermined. Ban-Na-Thoung, Laos. (figured specimen); Uralian, limestone with *Schwagerina princeps*, Bo-Sune.

Lithostrotion (*Waagenella*) *omiensis* Yabe and Hayasaka, 1915, p. 104. Upper Carboniferous or Permian, *Fusulina* Limestone. Ômi, Nishi-Kubiki-gôri, Province Edrigo.

Lonsdaleia (*Waagenella*) *hupeiensis* Yabe and Hayasaka, 1915, p. 105. Carboniferous, beds with *Fusulinella* and *Macro-*

porella. Fu-shan coal-mines, Lung-chi-ang-chen Wu-chang-fu, Province Hupei.

Genolectotype.—*Lonsdaleia indica* (Waagen and Wentzel), 1886, p. 897, pl. 101, figs. 1–3, pl. 115, figs. 3–4. Permian, Upper *Productus* Limestone. Various localities, Salt Range, India. See Grabau, 1931, p. 42; and Huang, 1932, p. 46.

Diagnosis.—Phaceloid and cerioid rugose corals with typically a clisiophylloid axial column[4] which almost fills the tabularium,[5] more or less horizontal tabulae sometimes suppressed, large, steeply inclined dissepiments, and septa which reach the epitheca and are united at their peripheral edges by stereome to form a narrow stereozone.[6] Germination is non-parricidal.

Remarks.—The diagnosis given above has the genotype more particularly in view. Other species of *Waagenophyllum* may differ from *W. indicum* in some important detail, and may exhibit characters not found in Waagen and Wentzel's species. The presence of small globular dissepiments, not included among the diagnostic characters of the genus, may be mentioned. These are very feebly developed and not always present in *W. indicum*, but form a very definite outer border in the species from Chitral described on p. 37, and entirely replace the large dissepiments in the form from Keremeos. Yabe and Hayaska (1916, p. 96) define *Waagenophyllum* (under the name *Waagenella*) as follows:

> Corallum composite, fasciculate or massive. Corallites cylindrical or prismatic. Columella considerably thick, composed of more or less twisted, vertical, radial lamellae and closely set, conically-elevated tabulae; other characters as in *Lithostrotion*.

This diagnostic description is correct as far as it goes but it omits some of the most distinctive features of the corals and implies a relationship with *Lithostrotion*, whereas there can be little doubt that they are allied not to *Lithostrotion* but to *Lonsdaleia*. Huang (1932, p. 43) considered this to be the case when he placed *Waagenophyllum* in the Lonsdaleidae.[7] Huang notices (p. 46) the most outstanding characters of the genus, and remarking on the difference between *Waagenophyllum* and *Corwenia* (p. 46) says:

> The chief difference lies in the character of the tabulae. In *Waagenophyllum* the tabulae are practically absent but in this subgenus (*Corwenia*), they form a wide tabulate zone surrounding the columella.

[4] The axial column ("central column," Smith, 1913, p. 59) is a complex structure formed of vertical and transverse elements and occupies the axial region of the coral. The transverse elements, the tabellae (Smith, 1916, p. 225), small plates derived from the tabulae, are superposed one upon another and are traversed by the vertical lamellae, which are the isolated ends of septa. In the clisiophylloid type of axial column there are approximately as many lamellae as there are major septa and a medial plate, which is only thickened near the axis and thus in transverse section appears short. In the dibunophylloid type on the other hand, there are few septal lamellae, but the medial plate is thickened more or less throughout and bisects the column. These two types of axial columns grade into one another and there are many variations in details. Individual corallites of the same colony often differ considerably from one another in the "pattern" of the axial column.

[5] *Tabularium* (Lang and Smith, MS). This term, used here for the first time, has been suggested by W. D. Lang to denote the part of a coral occupied by the tabulae or tabellae, and is defined by the surrounding wall of dissepiments.

[6] *Stereozone* (Lang and Smith, 1927, p. 456), the peripheral part of a coral which has been rendered solid either by lateral contact betwen dilated septa or by the deposition of stereome between the septa.

[7] I cannot agree with him in including the simple clisiophyllids, *Dibunophyllum*, etc., in the same family. The resemblances between these and the lonsdaleidoid corals are in my opinion brought about by parallel evolution. It is quite clear from a careful examination of the various corals in which an axial column is developed that this structure is evolved independently in a number of lineages. Mr. Huang is quite right in pointing out that the coral figured by T. H. Ryder and myself in *Ann. Mag. Nat. Hist.*, ser. 9, vol. 17, pl. 6, (also pl. 1, fig. 6) is a species of *Waagenophyllum*; in fact, it is a typical although small, form of *W. indicum*. At the time we published the paper I was not certain of the characters of the Indian coral, and Mr. Huang is mistaken in thinking that I do not accept the genus.

Corwenia, I would add, has a more loosely formed central column and small dissepiments only. It is probable that the Permian species of *Corwenia* from Southern China are more closely allied to those of *Waagenophyllum* than they are to the genotypes of *Corwenia rugosa* M'Coy, Lower Carboniferous, Britain.

Since the genera *Lonsdaleia* and *Corwenia* are mentioned in considering *Waagenophyllum* and are referred to elsewhere in this paper, brief details of these must also be given:

Lonsdaleia M'Coy (1849, p. 11).

Genotype (by designation): "*Erismatolithus Madreporites* (*duplicatus*)" Martin (1809, pl. 30, figs. 1–2). Carboniferous, Viséan, Derbyshire, England.

Diagnosis.—Phaceloid, cerioid, and even plocoid,[8] rugose corals with an axial column resembling that in *Dibunophyllum* or *Clisiophyllum* and typically with horizontal tabulae and large dissepiments imperfectly traversed by the septa and forming a wide peripheral zone.

Remarks.—See S. Smith (1916) for a detailed account of the structure of these corals.

Corwenia Smith and Ryder (1926).

Genotype (by designation): *Lonsdaleia rugosa* M'Coy (1849, p. 13; 1851, p. 105, pl. 3B, figs. 6, 6a–c). Carboniferous, Viséan, [Hafod-y-Calch] Corwen, North Wales.

Diagnosis.—Phaceloid rugose corals with an axial column similar to that in *Lonsdaleia*, but with peripherally inclined tabulae, small dissepiments and septa which extend to the epitheca.

Remarks.—For further information see S. Smith (1916, pp. 264–268) and Smith and Ryder (1926). The diagnosis given in the later work reads "Compound rugose corals, which possess to a greater or lesser degree the internal structures of *Dibunophyllum* Nicholson and Thomson." Though this is true, close relationship between species of *Corwenia* and *Dibunophyllum* must not be assumed. The homeomorphy in structure is more probably due to evolution along parallel lines.

Before describing the coral from Keremeos it will be profitable to consider *Waagenophyllum indicum* and certain other phaceloid forms of *Waagenophyllum* from the Tethys, for this will render it much easier to show in what respects *W. columbicum* agrees with and differs from the more typical members of the genus. Moreover, *Waagenophyllum indicum* is an important coral, and although it has already been discussed by several writers, room still remains for further remarks. Only three of the several phaceloid species of *Waagenophyllum* and none of the cerioid forms are noticed here, although the latter include some very interesting corals.

The publications mentioned on pp. 41–42, include, however, most of the works in which species of *Waagenophyllum* have been described.

WAAGENOPHYLLUM INDICUM (Waagen and Wentzel)[9]

Lonsdaleia indica WAAGEN AND WENTZEL, *1886*, p. 897, p. 101, figs. 1c–d, 2, 3a–b; pl. 115, figs. 3, 4.—DIENER, *1897*, p. 82, pl. 13, figs. 5, 6a, b.—ENDERLE, *1900*, p. 94.—SCHELLWIEN, *1905*, p. 358.—DIENER, *1911*, p. 43, pl. 6, figs. 4a–b.

Lonsdaleia virgalensis WAAGEN AND WENTLEL, *1886*, p. 900, pl. 101, fig. 4; pl. 116 figs. 2a–c.

Lonsdaleia sp., form between *L. indica*, and *L. virgalensis*, LOCZY AND FRENCH, in Széchenyi, *1897*, pp. 88 and 199, pl. 5, figs. 8a–d.

Waagenella indica (Waagen and Wentzel), YABE AND HAYASAKA, *1915*, p. 96.

Lonsdaleia cf. *indica* Waagen and Wentzel, ALBRECHT, *1924*, p. 293.

Waagenophyllum indicum (Waagen and Wentzel), HAYASAKA, *1924*, p. 23.

Lithostrotion jourdyi MANSUY, *1912*, p. 69, pl. 13, fig. 5.

[8] A plocoid corallum is one in which the contiguous corallites are not separated by epitheca and are united by their confluent septa and dissepimental tissue or by dissepiments only. The plocoid species of *Lonsdaleia* are placed by Yabe and Hayasaka (1916, p. 63) in a separate genus, *Polythecalis*, genotype, *P. confluens* Yabe and Hayasaka (*op. cit.*, p. 65), "Carboniferous?", China.

[9] For references in synonymy see the Bibliography at end of paper.

Lonsdaleia cf. *indica* Waagen, SIMICA, *1932*, pp. 30, 51.

Waagenophyllum virgalense (Waagen and Wentzel) var. *mongoliensis*, GRABAU, *1931*, p. 42, pl. 1, figs. 8a–d, 9a–c.

Lonsdaleia indica Waagen, MANSUY, *1912*, p. 9, pl. 1, figs. 3a–c.

Lonsdaleia indica (Waagen and Wentzel), SMITH in Reed, *1925*, pp. 14–16, pl. 1. figs. 24–27.

Lonsdaleia (*Waagenophyllum*) *indica* var. *akagoensis* OZAWA, *1925*, p. 76, pl. 14, figs. 7, 8, 9.

Diagnosis.—Slender phaceloid *Waagenophyllum* in which the axial column almost but not quite fills the tabularium, most of the dissepiments are very large and very steeply inclined, and a stereozone is well developed.

Description.—The corallum is formed of tall, straight, cylindrical corallites 4 mm. to 8 mm., though more generally about 5 mm., in diameter, growing parallel and in close proximity to one another, and joined at irregular intervals by horizontal connections. Three small radiciform outgrowths also give rise to the young corallites as illustrated by Waagen and Wentzel's very clear figure (Pl. 115, fig. 4). There are 40 to 44 septa. The major septa extend almost but not quite to the axial column and end abruptly or become extremely attenuated at a short distance from it. Occasionally however, the end of a septum may continue into the column as one of the vertical lamellae. The minor septa are about half or less than one half the length of the major but are often much thinner. The septa dilate peripherally but only for a very short distance from the epitheca and the dilated parts are welded into a narrow stereozone by the interstitial stereome. The axial column occupies nearly one third and the whole tabularium approximately one half of the corallite. Thus the tabulae are restricted to an exceedingly narrow zone while the dissepiments form a relatively wide one. The axial column is compact, and well defined and closely resembles both in transverse and longitudinal section that of *Lonsdaleia floriformis crassiconus* M'Coy (S. Smith, 1916, pl. 20, figs. 5–8). It is built up of sloping, conical tabellae, about 6 in 1 mm., incompletely bisected by a short thickened medial plate and traversed by approximately as many vertical lamellae as there are major septa.

The tabulae which lie more or less horizontally are very much more widely and more unevenly spaced than the tabellae of the axial column. Except sometimes near the periphery of the corallite, where a few small globose dissepiments of the more usual kind may be developed, the dissepiments are exceptionally long, only slightly curved, and very steeply inclined, in fact often almost vertical. They extend into the horizontal outgrowth, bending around, however, into a horizontal position in order to do so.

Remarks.—In *Waagenophyllum indicum* several very distinctive characters are well developed and it is admirably suited to be the genotype of this important genus. In most of the other species of *Waagenophyllum* some one or another of the characteristic features is less pronounced or may even be absent or, on the other hand, may be exaggerated. The wide geographical range of *W. indicum* adds considerably to the stratigraphical value of the species.

Waagen and Wentzel, considering the time at which they wrote, give a very clear description of the coral. They state that the corallites do not exceed 6 to 8 mm. in diameter and make the following observations of particular interest: "Septa not numerous, about 20 primary and as many secondary septa, all uniting at the periphery to form a distal outer wall. [Thus noticing the stereozone] . . . It is remarkable that in longitudinal section barely any tabulae can be observed outside of the columella, unless the steeply ascending lines in pl. 101, fig. 3c, on both sides of the columella should be considered not as irregular cut septa but as tabulae." As a matter of fact the steeply ascending lines are the large dissepiments.

It should be pointed out here that their

figures of the longitudinal sections on pl. 101 are the wrong way up, and this reversed orientation explains certain misleading statements in their description.

Horizons and localities.—Permian. The species was first described from the Upper and Middle *Productus* Limestone, Salt Range, India (Waagen and Wentzel, 1886), and has been subsequently obtained from equivalent beds in Mongolia (Grabau), Sze Chwan, S. W. China (Loczy and Frech, 1897), Himalayas (Diener, 1897), Shan States (Diener 1911), Badia Madan, Asia Minor (Enderle, 1900), West Serbia (Albrecht and Simica, 1924). *Waagenophyllum indicum* var. *kueichowensis* Huang from Southern China is closely allied to *Waagenophyllum indicum*, s. str, differing slightly from it in unimportant details. Mansuy's *Lithostrotion jourdyi*, which appears to be the same coral, is recorded from the Carboniferous of Indo-China, but no other fossils are mentioned and therefore it is probable that the beds from which the coral was obtained are also Permian.

I am indebted to Doctor W. D. Lang and Mr. A. G. Brighton for the loan of specimens and sections of the coral from the Salt Range in the collections of the British and Sedgwick Museums. Professor Franz Heritsch has also been good enough to send me a specimen which he collected in the *Bellerophon* Limestone, Upper Permian, Bastarsko. Brdo, West Serbia. The Serbian specimen is a typical though small form, the largest corallites being only 5 mm. in diameter, and is somewhat of a dense texture, the solid and opaque character of the coral being probably not an original feature, but due to mineral changes.

WAAGENOPHYLLUM AKASAKENSE (Yabe)

Lonsdaleia akasakensis YABE, *1902*, p. 4, text fig. on p. 5.

Lonsdaleia (*Waagenella*) *akasakensis* Yabe, YABE AND HAYASAKA, *1915*, p. 100.

Lonsdaleia (*Waagenophyllum*) *akasakensis* Yabe, OZAWA, *1925*, p. 75, pl. 14, figs. 5 and 6.

Diagnosis.—Phaceloid *Waagenophyllum* differing from *W. indicum* in having slightly stouter and more twisted corallites, an axial column which occupies the whole tabularium, longer minor septa, and a greater development of small dissepiments.

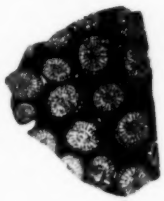
Description.—The species is similar to *Waagenophyllum indicum* in most respects, but differs from it in a few details. The corallites, 4 to 12 mm. in diameter, are rather flexuous and are rather more widely separated. It has 40 to 48 septa, of which the minor are nearly as long as the major; the former attain two-thirds to four-fifths the length of the latter but are

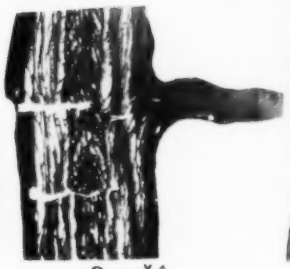
EXPLANATION OF PLATE 8

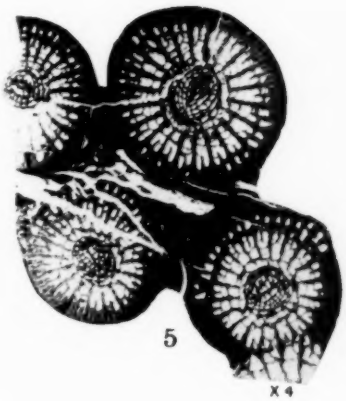
FIGS. 1–6—*Waagenophyllum indicum* (Waagen and Wentzel). 1–4, Specimen R. 6589, British Museum (Koken coll.), middle *Productus* limestone, upper zone, Virgal, Salt Range, Punjab, India; 1, transverse section, R. 29985, ×4; 2, same, nat. size; 3, longitudinal section, R. 29989, ×4; 4, longitudinal section, R. 29990, ×4; note the lateral process connecting the two corallites in fig. 1, developed from the side of the corallite in fig. 3, and a young corallite rising from a similar process in fig. 4. 5, Transverse section A. 4610c, ×4, Sedgwick Museum, Cambridge; Permian, middle *Productus* limestone, south side of Jarhanwala Nala Valley, path from waterfall to Kumaranwali Dhok, about 1¾ miles N.E. of Warcha Mandi, western Salt Range, India (See Reed, 1930). 6, Transverse section of smaller variety, R. 22380, ×4, British Museum, locality unknown [Permian, Tethys]. (p. 34)

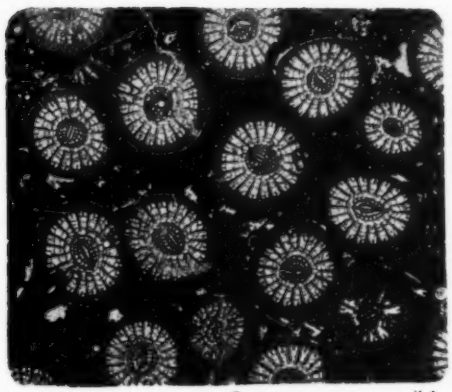
7, 8—*Waagenophyllum chitralicum* Smith, n. sp., right bank of Yarkhun River, 2½ miles north of Baroghil Ailak, N.W. Province, Chitral, India. Sections in British Museum cut from holotype in the collections of the Geological Survey of India; 7, transverse section, R. 27870, ×2; 8, longitudinal section, R. 27871, ×2; see also Reed, 1925, pl. 1, figs. 24–27. (p. 37)

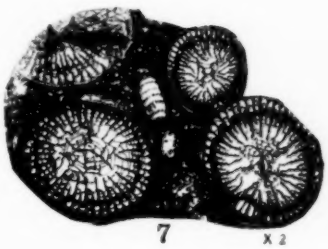
9—*Waagenophyllum columbicum* Smith, n. sp., holotype, Nat. Mus. Canada cat. no. 9059, Keremeos, British Columbia. Transverse section, ×4, included here so that it may be more readily compared with that of *W. indicum*. (p. 38)

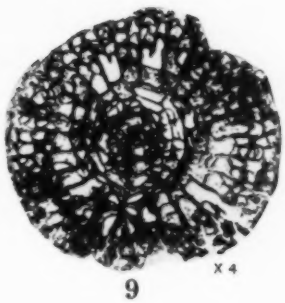












Smith, Anthracolithic corals

usually much thinner. The axial column entirely fills the tabularium. The inner dissepiments are similar in character to those in *W. indicum* though perhaps less elongated, not quite so steeply inclined, and slightly more arched. Small dissepiments form a wider and more persistent peripheral border.

Remarks.—The interesting feature of *W. akasakense* is in the complete crowding out of the tabulae by the axial column. My information respecting the species has been partly obtained from the clear descriptions of it given by the Japanese author, and partly from sections of a topotype specimen very kindly sent to me by Professor Ichiro Hayasaka, which, as far as a single specimen can, entirely confirms former descriptions based on more ample material.

Horizon and Locality.—Permian, *Neoschwagerina globosa* limestone, Kinshôzan, Akasaka, Province of Mino, Japan.

WAAGENOPHYLLUM CHITRALICUM Smith, sp. nov.

Plate 8, figures 7, 8.

Lonsdaleia indica Waagen and Wentzel, SMITH in Reed, *1925*, pp. 14–16, pl. 1, figs. 24–27.

Diagnosis.—Phaceloid *Waagenophyllum* with an axial column which is more loosely formed and does not occupy so much of the tabularium as that of *W. indicum* and has a twisted medial plate. The tabulae and both the inner (large) and outer (small) dissepiments are all well developed.

Description.—The straight cylindrical corallites attain a diameter of about 8 mm. The axial column is approximately 2.5 mm. in diameter but varies; in some places it almost fills the tabularium, but in others leaves room for quite well developed tabulae. It is more loosely constructed than that of *W. indicum* in every way, and is more circular in transverse section; the medial plate is twisted and often inconspicuous. The tabulae are horizontal or slope slightly inwards towards the column, and on an average are about 0.5 mm. apart. The inner dissepiments are large, as in *W. indicum*, but are not so elongated or so steeply inclined and are more curved. The outer dissepiments, although mostly small and globose, include some which are much longer and less arched than the rest. The inner dissepiments form a zone 1.5 to 2 mm. and the outer series a zone 1 to 1.5 mm. wide. There are about 48 septa. The major septa extend almost to the axial column and occasionally even invade it. The minor septa attain half to two-thirds the length of the major. The peripheral parts of the septa are only sometimes dilated and a stereozone, if developed at all, is not necessarily continuous round the whole circumference of the corallite.

Remarks.—*Waagenophyllum chitralicum* is founded here on a small group of corallites which I described on a previous occasion as *Lonsdaleia indica* Waagen & Wentzel, but which are larger than most specimens of that species and differ from them in a number of details. In its well developed outer zone of small dissepiments *W. chitralicum* approaches nearer to the *Waagenophyllum* from Keremeos than any of the other forms of the genus mentioned in this paper.

The holotype is a piece of dark grey limestone measuring originally 12×16 ×3.5 cm. The specimen and most of the sections cut from it are in the collections of the Geological Survey of India, but the two sections figured here are in the British Museum.

Horizon and Locality.—Upper Carboniferous, Uralian, Chitral, right bank of the Yarkhun River about 2 miles north of Baroghil Ailak. I am here including the whole of the Uralian in the Upper Carboniferous though recognizing that some authors place its upper part in the Lower Permian. Reed (1925, p. 134) discussing the fossils from Chitral remarks: "This fauna has a general facies and composition similar to that occurring in the *Schwagerina* Stage and to a less extent the *Cora* Stage of the Urals and is characteristic of uppermost beds of the Upper Carboniferous."

WAAGENOPHYLLUM COLUMBICUM
Smith, sp. nov.
Plate 8, figure 9; Plate 9, figures 1–10

Diagnosis.—Large *Waagenophyllum* in which the axial column is incompletely differentiated from the peripherally sloping tabulae and small globose dissepiments only are present.

Description.—The corallites 10 mm. to 17 mm. in diameter, are tall and straight, lie close together and often touch one another. In a corallite of 13 mm. diameter (the average dimension), the tabularium is about 8 mm. and the axial column about 5 mm. in diameter. The axial column is formed of closely packed tabellae (four or five in the space of 1 mm.), which slope at an angle slightly exceeding 45°. In transverse section the column is oval, encloses a short medial plate, and is imperfectly radiated by nearly as many vertical lamellae as there are major septa. The tabulae slope in the same direction as the tabellae, but not so steeply and less regularly, and are more widely and irregularly spaced. Many of them bend round near the wall of the tabularium in the form of the letter U. Most of the tabulae abut against the tabellae which form the axial column but some are actually continuations of these into the medial zone. Surrounding the tabularium is the peripheral zone formed of three or four series of small, but by no means uniform, dissepiments corresponding to the outer dissepiments in the other species of *Waagenophyllum* described here. There is no trace of the large, steeply ascending dissepiments so characteristic of the genus unless these are represented by the steeply upturned peripheral edges of the tabulae.

There are about 50 septa; the major septa, as in other species of *Waagenophyllum*, extend nearly to the central column; the minor septa usually attain half the length of the major. The septa attenuate peripherally and become slightly wavy. Miss Dorothy Hill, of Newnham College, Cambridge, who has made a close study of the microscopic structures of rugose corals and has seen my sections of *W. columbicum* has pointed out that in transverse section the septa show the axially curved banding which is very characteristic of well preserved Permian corals.

Remarks.—*W. columbicum* is not a typical member of the genus *Waagenophyllum*. It is much larger than any of the species that have been described from Asia, and it differs from the genotype more, in most of its structures. Nevertheless it possesses the large axial column and reduced tabulae which are so distinctive of the genus. The individual corallites even in the same corallum vary quite widely from one another in details.

Specimens.—Holotype, National Museum Canada cat. no. 9059; paratypes, (I) N. M. C. cat. no. 9060, (II) N. M. C. no. 9061.

Horizon and Locality.—Permian (or possibly Upper Carboniferous) crinoidal limestone. Ridge between Blind and Barslow Creeks, near Keremeos, Similkameen District, British Columbia, Canada.

CANINIA Michelin, 1840

Caninia MICHELIN, in Gervais, *1840*, p. 485.

Genotype.—By designation, *Caninia cornucopiae* Michelin in Gervais (1840, p. 485). [Lower Carboniferous] Sablé, N.W. France (?), and Tournay, Belgium—"dans des terrains de formation secondaire, à Sablé (Sarthe), en Belgique, etc." Described and figured by Michelin (1847, p. 256, pl. 59, fig. 5) who gives one locality only, Tournay—"Fossile de Tournay (Belgique)."

Carruthers (1908, p. 166) and Bather (1908, p. 288) consider that the locality Sablé was wrongly included by Gervais since this place is not mentioned by Michelin, and Michelin (1841, p. 81) states "dans les localités de Juigné, Sablé et Solesme, on ne rencontre ordinairement soit dans les bancs schisteux, soit dans les couches de marbre exploité, que l'espèce ci-après nommée *Caninia gigantea*."[10]

[10] The Carboniferous beds at Sablé lie slightly higher in the series than those at Tourney.

Diagnosis.—Simple trochoid and cylindrical corals in which, except in very early states, the septa do not reach the axis, the cardinal fossula is generally wide and conspicuous, the tabulae are mostly complete, and dissepiments are present.

Remarks.—The name *Caninia* was first published by P. Gervais in an article on the Astreaea (Dict. Sci. Nat. Suppl. 1, 1840, p. 485[11]). He attributes the genus to Michelin, "Congrès de Turin, 1840." The Proceedings of the Congress were not printed, however, until 1841. Gervais most probably obtained his information from Michelin personally. His remarks on the genus are considerably fuller than the brief reference to *Caninia* in the report of the Turin meeting, in which no species are given. Gervais expressly mentions *C. cornucopiae* Michelin as the type, but this species was not described until 1847, when Michelin described and figure material from Tournay in his *Iconographie.*

Caninia is an important genus in the Lower Carboniferous of eastern Europe, and includes a wide range of forms, which however, grade into one another. The genotype is a small coral with few dissepiments, but in the large *Caninia gigantea* Michelin (1843, p. 81, pl. 16, fig. 1) the tabularium is bordered by a wide zone of dissepiments imperfectly traversed by the septa. *Caninia* ranges up into the Permian and down into the Devonian, but it is possible that the older and younger caninioid corals may have developed independently from different zaphrentid ancestors.

Campophyllum Edwards & Haime (1850, p. 68) and *Siphonophyllia* Scouler in M'Coy (1844, p. 187, pl. 27, fig. 5) are synonymous genera, although founded on species of *Caninia* other than *C. cornucopiae. Caninia* differs from *Amplexus* Sowerby (1814, p. 165) in having longer septa and more closely packed tabulae, and in possessing dissepiments.

For the history of the genus and for a good description of the genotype see Carruthers (1908), and for description and figures of other species of *Caninia*, see Saleé (1910), and Lewis (1924).

Caninia sp.

Plate 9, figure 11

Description.—The corallum, 4.5 cm. in diameter through the calice and 10 cm. long, is incomplete, 2 mm. or more are missing from the proximal end and the distal part was also imperfect. The epitheca and most of the dissepimental zone had been destroyed (except at one place near the calice) even before the coral was incorporated in the limestone, and on one side the fossil had been still more deeply corroded through weathering in the rock face. The specimen has been cut and part of it used in preparing sections.

There are between 50 and 60 major septa which extend well into the tabularium but leave unoccupied an area about 10 mm. in diameter at the axis. Although the septa appear to have reached the epitheca, their peripheral parts, which lie outside the tabularium, are extremely thin. Within the tabularium, however, they are very strongly dilated and for some distance are to a great extent in lateral contact, but they taper axially to a fine edge and become very much twisted. The minor septa are very short and thin and do not extend inwards as far as the tabularium. The cardinal fossula is well marked. The tabulae, most of which are complete, are fairly close together, but the intervals between vary—at some levels they are crowded, but at others rather widely spaced. The dissepiments form a peripheral zone 10 or 12 mm. wide in the distal part of the corallum.

Remarks.—The coral is a very typical *Caninia* but is without any very outstanding characters and is too imperfect to name. Its most distinguishing features are perhaps its very much twisted septa.

[11] F. A. Bather (1908, p. 288) suggests that Gervais' article was not actually published until 1841 although the work is dated 1840, but there is no evidence or any reason to suppose this was the case.

The type of septal dilation seen in this is very characteristic of *Caninia*, though very often the thickening is confined entirely to the septa on the cardinal side of the corallum. The Canadian form does not differ very greatly from *Caninia juddi* Thomson, emended Lewis, common in the Viséan (upper division of the Lower Carboniferous) of Britain (see Lewis, 1924, pls. 27–30), but somewhat similar forms also occur in the Upper Carboniferous of Central Russia, the Urals, and Timan (see Stuckenberg, 1904, 1895).

Several species of *Caninia* have been described from the Permian of Tethys; From Timor, by Gerth (1921, pp. 97–98, pl. 146, fig. 24), and Koker (1924, pp. 12–14, text fig. 9 & 10, pl. 4, figs. 1–5); and from South China by Huang (1931, pp. 35–39, pl. 1, figs. 8–14).

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I tender my most cordial thanks to all those from whom I have had help whilst preparing this paper—to Doctor E. M. Kindle, Chief of the Palaeontological Division, Canadian Geological Survey, for sending me the interesting corals from British Columbia and for bringing to my notice recent publications on other Anthracolithic fossils found in this province; and to Mr. A. G. Brighton, Professor Franz Heritsch, Professor Ichiro Hayasaka, Doctor W. D. Lang, and Doctor F. R. C. Reed for Tethyan material, including the loan of specimens in the British and Sedgwick Museums. To Mr. A. Sen, of Calcutta, I am indebted for a fine topotype from the Salt Range. I thank Profesor Heritsch, Doctor Reed and Doctor H. Dighton Thomas with whom I have discussed various matters concerning Anthracolithic faunae and correlations, for much useful information and for their valued opinions. To Doctor Thomas I am deeply indebted for the ungrudging assistance he has given me in other ways, particularly for his help with the literature and in verifying my references, a task which it was impossible to carry out unaided at Bristol.

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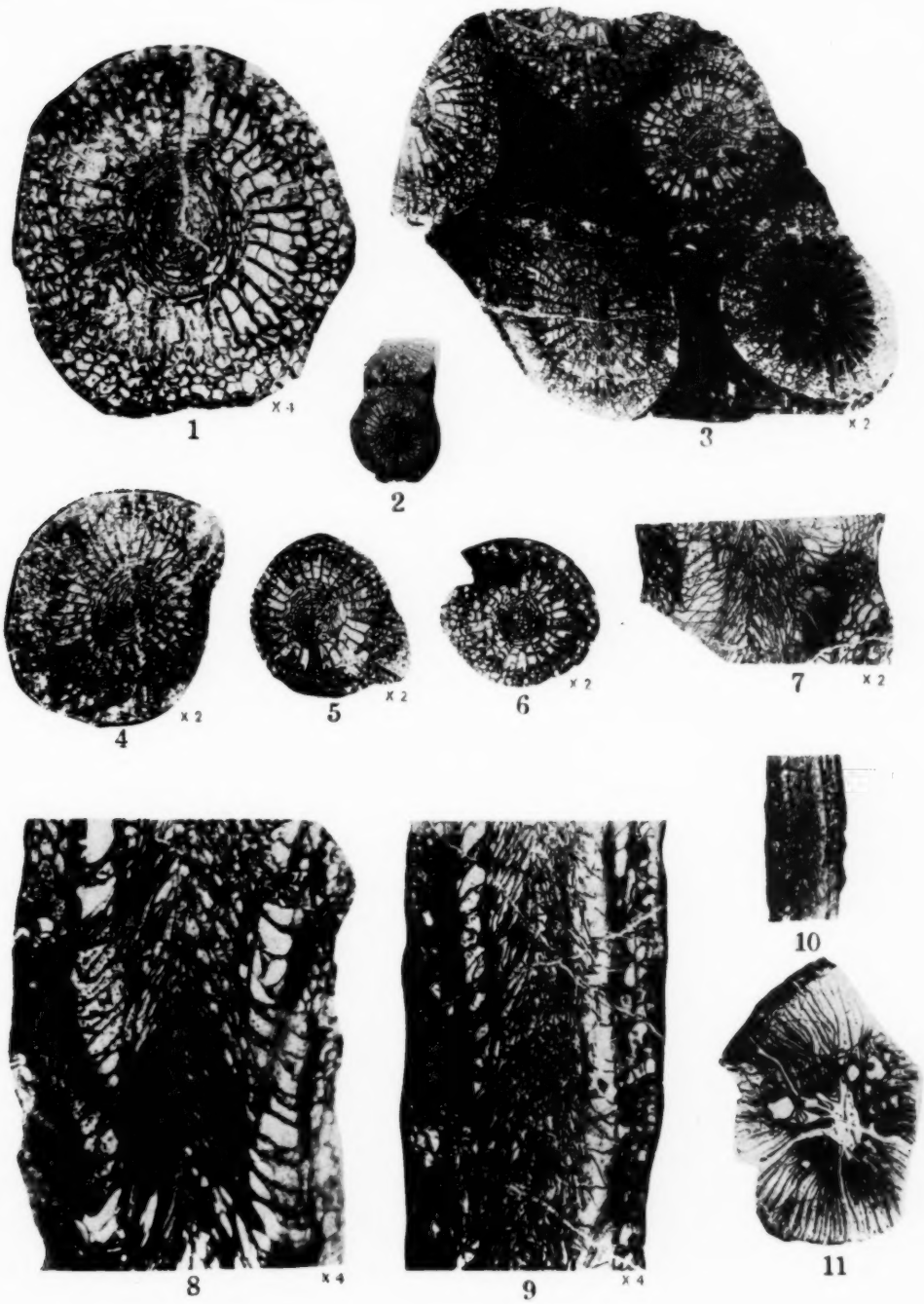
EXPLANATION OF PLATE 9

FIGS. 1–10—*Waagenophyllum columbicum* Smith, n. sp., Permian (or Upper Carboniferous), ridge between Blind and Barslow Creeks, 4 miles east of Keremeos, British Columbia. All sections in collections of the Nat. Mus. Canada. 1, 2, 5, 6, 8, holotype, N. M. C. cat. no. 9059; 1, transverse section, ×4; 2, same nat. size; 5, 6, transverse sections, ×2; 8, longitudinal section, ×4. 3, 4, 7, 9, 10, paratype, N. M. C. cat. no. 9060; 3, 4, transverse sections, ×2; 7, longitudinal section, ×2; 9, longitudinal section, ×4; 10, same, nat. size. (p. 38)

11—*Caninia* sp., same locality and horizon as figs. 1–10. Transverse section, nat size. (p. 39)



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CHEMUNG TRACKS AND TRAILS FROM PENNSYLVANIA[1]

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ABSTRACT

Certain tracks, from shales whose age is unquestionably fixed as early middle Chemung (Late Devonian), are believed to have been made by primitive, semi-terrestrial vertebrate animals whose fore-limbs were still fin-like and whose hind-limbs had evolved into true legs with five-toed feet. These animals, here named *Paramphibius*, are believed to have developed from small, unknown crossopterygian ganoids and to have been directly or indirectly ancestral to the succeeding true amphibians of the Carboniferous because they were anatomically and in habits intermediate between the two groups. The environment was largely fresh-water, but *Paramphibius* was capable of making trips on land. It is believed that the order of change from fins to feet was first hind-limbs, then fore-limbs. Annelid and arthropod trails and plant debris accompany the vertebrate tracks.

In the summer of 1931 the writer spent two days in the field with Mr. D. S. Harding of Susquehanna, Pennsylvania, who for years has made the study of the geology about his home an avocation. Mr. Harding at that time mentioned having observed certain Chemung fossils which he thought might be foot-tracks. He had none on hand, but promised to secure some. Accordingly, three slabs bearing curious little markings arrived at Harrisburg the following winter. The writer at first doubted their being actual foot-tracks, but study of additional specimens has convinced him that Mr. Harding's original suggestion is correct. They are tracks and trails of small animals; some are believed to be unquestionably of vertebrate origin. Realizing their significance the writer again visited Mr. Harding in 1932, and together they collected many more tracks. Mr. Harding has since sent in additional material, and another joint collecting trip was made in the spring of 1934. Entire credit for the discovery of these fossils must go to Mr. Harding, who has himself collected or helped collect all of the specimens now in the possession of the Pennsylvania Topographic and Geologic Survey.

The unique nature of these fossils has caused the writer to hesitate to describe them. The dissimilarity to any known tracks makes classification difficult. However, after nearly three years of deliberation, after exhibiting photographs of the tracks at the 1932 meeting and some of the specimens at the 1933 meeting of the Geological Society of America and hearing the comments they elicited, and after discussing the tracks upon various occasions with several vertebrate paleontologists, it has been de-

[1] Published by permission of the State Geologist of Pennsylvania. Manuscript received June 13, 1934.

cided to publish an account of these remains. The conclusions may be in error and certainly should not be considered final; comment and suggestion will be welcomed. Final proof must await discovery of actual skeletal remains.

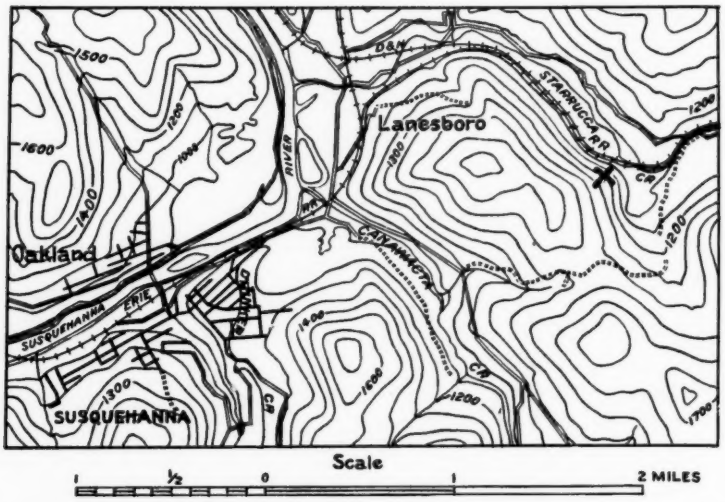


FIG. 1—Detail from uncorrected advance topographic sheet, Susquehanna Quadrangle, Pennsylvania and New York, United States Geological Survey, showing location of quarry (×) where tracks were obtained.

OCCURRENCE

Location.—All of the tracks herein described were collected in an abandoned flagstone quarry on the south slope of Starrucca Valley, about 1½ miles east of Lanesboro. This quarry is at an elevation of approximately 1,200 feet above sea level, and 300 feet above the Susquehanna River at Lanesboro.

Stratigraphy of northeastern Susquehanna County.[2]—Over half a century ago I. C. White published his Starrucca Creek section.[3] This has been carefully checked by Mr. Harding and found sufficiently accurate to be adopted now as a summary of the local stratigraphic succession. It is quoted here just as White published it.

Starrucca Creek Section

		Feet
1.	*New Milford* lower sandstone,	25
2.	——————concealed,	65
3.	Sandstone,	5
4.	Gray shales,	5
5.	Sandstone, gray,	4
6.	Gray, sandy shales,	6
7.	Somewhat massive sandstone,	30
8.	Olive shales with *Chemung shells near base*,	125
9.	Olive sandstone with a layer of quartz conglomerate near the middle 1 foot thick,	8
10.	Olive shale,	8
11.	Olive sandstone,	4
12.	Olive shale with a layer of *iron ore* near the middle,	40

[2] Mr. D. S. Harding furnished most of the stratigraphic notes incorporated in this article. The value of his knowledge of the local geology can hardly be overestimated.

[3] White, I. C., The geology of Susquehanna county and Wayne county: *Second Geol. Survey Pennsylvania, Rept.*, vol. G5, p. 97, 1881.

13. *Brick red shale*,..... 10
14. ———— concealed to Susquehanna River and containing the *Cascade Creek sandstone* near its center, . . . about..... 100

The Cascade Creek sandstone (number 14 in part) carries a lower Chemung marine faunule at its type locality on Cascade Creek, 2 miles north of Lanesboro.[4] Mr. Harding collected marine invertebrates from an outcrop below the foot-track quarry on the railroad in what he believes to be White's number 12. From this collection the following have been identified: *Camarotoechia horsfordi* (Hall), *Spirifer disjunctus* Sowerby, *S. mesastrialis* Hall, *Modiomorpha* cf. *M. arcuata* Hall, *M. subalata* var. *chemungensis* Hall, *Goniophora* sp., *Cypricardella* sp. Since he also found this zone near the forks of Drinker Creek about one mile south of Susquehanna village, these occurrences may represent a useful, local datum.

Many of the tracks are preserved in fine, even-textured, greenish shale which breaks into thin slabs along the smooth bedding surfaces (see Pl. 11, fig. 1). Minute details are rendered exceptionally clear in this medium. Some fine-grained, greenish or gray-green sandstone beds are present, too, and part of the shale is finely arenaceous. These media fail to preserve the finer details of the tracks. The track-bearing shale occupies the lower part of White's concealed number 2 and forms the base of a 30-foot face that is the uppermost rock of the abandoned quarry.

[4] White, I. C., *op. cit.* p. 78; and Willard, Bradford, Devonian faunas in Pennsylvania: *Pennsylvania Top. Geol. Survey, Bull.* G4, p. 31, loc. 30, faunule 63, 1932.

This is about 175 feet above what White considered the top of the Chemung and some 250 feet higher than the top of the Cascade Creek sandstone. The New Milford lower sandstone is poorly exposed approximately 60 feet above the foot-track shale. White's "Catskill' is now known to be largely the equivalent of the Wellsburg or upper Chemung, and the strata he designated as Chemung actually represent only the Cayuta, or lower, member of that formation. In the Starrucca Valley the interval between the Cascade Creek sandstone and the New Milford lower sandstone is about 300 feet. This interval includes those beds which are transitional between marine Chemung and continental Catskill phases of sedimentation. In it the lowest red beds appear. Marine organisms cease to be common above the Cascade Creek sandstone, and in the upper portion fossil remains of any kind are few, though these include the tracks. The highest marine invertebrates surely recognized in place in this region were found in a medium-grained, greenish-gray sandstone in White's number 3 immediately below the track-bearing shale. This faunule is as follows: Crinoid columnals, *Spirifer disjunctus* Sowerby, *Modiomorpha arcuata* var. *chemungensis* Hall, *M.* sp. The marine faunules, the stratigraphic succession, and the correlation of the local stratigraphy with that of adjacent regions place the foot-tracks in the upper Cayuta and make their age early Middle Chemung.[5] Because no marine fos-

[5] For a more detailed discussion of the age of these beds see Willard, Bradford, "Cat-

sils are known from the foot-track shales or higher beds in this region, because of the character of the fossils associated with the tracks, and because of the local stratigraphy, paleogeography and contemporary geologic history, it is believed that the beds were formed in fresh water. The strata are essentially flat-lying with little or no local disturbance of any kind.[6]

FOSSILS OF THE FOOT-TRACK SHALE

The Faunule.—Various organic remains and some inorganic objects were discovered in the track-bearing shale. Most of the fossils are probably new and require further study, but the tracks and trails have been critically examined and are here described. The list follows:

- Invertebrates
  - Annelid trails
  - Arthropod trails
- Vertebrates
  - Digitate tracks and trails
- Plants
  - Casts of vertical stems
  - Small stems with leaves or bracts attached
  - Carbonized stem fragments
  - Indeterminate fragments, possibly leaf impressions
  - Coal layer $\frac{1}{8}$ inch thick
- Pseudofossils
  - Mud flow ridges
  - Ripple marks or dimplings

DESCRIPTION OF SPECIES

INVERTEBRATA

ANNELIDA

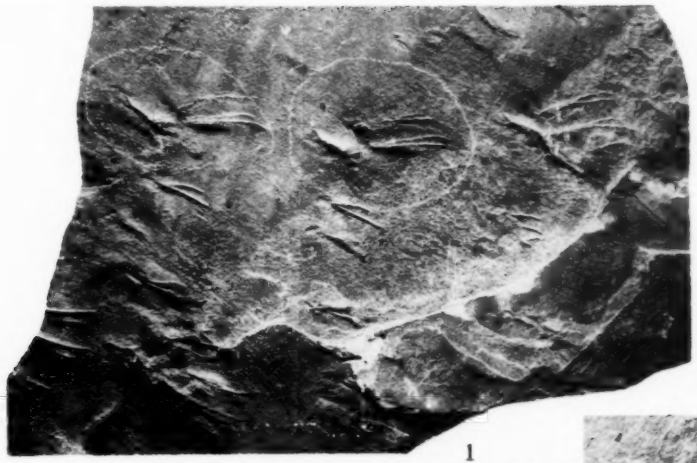
Two types of trails assigned to annelids occur. The first is a sinuous furrow about 1 mm. wide, presumably the work of a small "worm" crawling on soft mud. The second is a sinuous, very shallow, flat-bottomed trough 1 cm. wide. The bottom is rough, but too poorly preserved to show any recognizable pattern. Paralleling each edge of the trough and close to it is a single row of small, closely spaced, circular pits, each about 2 mm. in diameter and 1 mm. deep but lacking structural detail. The trail is thought to be that of a large chaetopod, although it might also be looked upon as possessing arthropod affinities.

skill" sedimentation in Pennsylvania: *Geol. Soc. Am., Bull.*, vol. 44, pp. 495–516 (particularly p. 506, loc. 9), 1933.

[6] Cathcart, S. H., Geologic structures in the plateaus region of northern Pennsylvania: *Pennsylvania Top. Geol. Survey, Bull.* 108, p. 17, 1934.

EXPLANATION OF PLATE 10

FIGS. 1–3—*Paramphibius didactylus* Willard, n. sp. 1, Fragment of a trail in which are impressed biramous "digits" of the fore limb (cf. fig. 3). There are also present fragments of other trails of this species and of *Paramphibius tridactylus*. Circles are drawn around the typical marks. 2, Trail of an adolescent individual showing the impressions made by the tail. Note the nodose character of the caudal groove, the overlapping of the foot tracks, suggestions of impressions of ventral armor, etc. In the curved portion of this trail the maker slipped sidewise, displacing the mud as a small mound, while the tail was deflected and the toes slipped. 3, Eight paces of a single trail. Of the fore limb, only impressions of a single, biramous "digit" registered (cf. fig. 1). The heel of the right pes is abnormal, and this abnormality is seen to recur in each impression, establishing the tetrapodous nature of the maker. All natural size. (p. 47)



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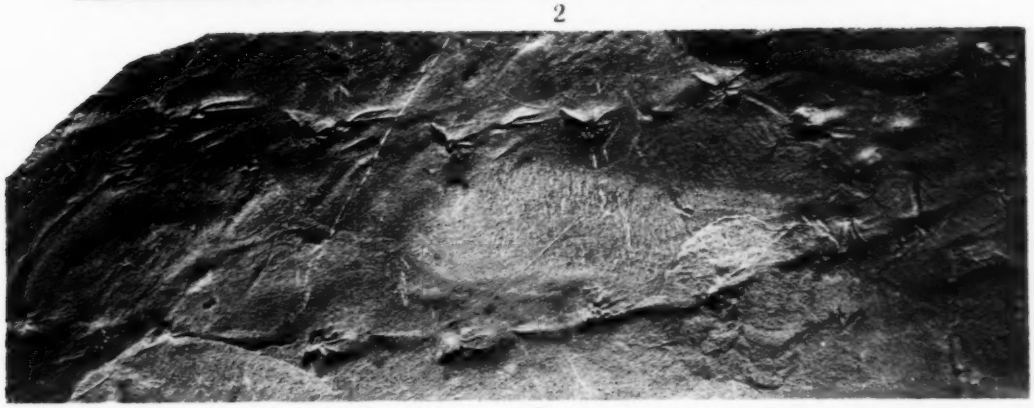


3

Willard, Chemung tracks

ARTHROPODA

A single trail presumably made by some unknown arthropod was found. It consists of a double row of oppositely arranged, symmetrical impressions, each of which is a smooth, slender, curved groove. Some of the grooves appear to have traces of setae along one edge. The trail is 15 mm. wide, and the average length of each single impression is 6 mm. The successive impressions are spaced about 3 mm. apart. It is presumed that these marks were made by some freshwater arthropod, doubtless a crustacean of some sort, but too little is known of the trail to offer further suggestions.

VERTEBRATA

Class AMPHIBIA

Order ICHTHYOPODA Willard, n. order

Primitive, fish-like Amphibia, known only from tracks and trails. Manus fin-like with varying number of bifurcating fin rays; pes pentadactylous.

PARAMPHIBIUS Willard, n. gen.

Tracks and trails, the maker of which possessed a fin-like manus carying biramous fin rays, and a pentadactyl pes with elongated third and fourth digits and a long heel. The generic name, coined by Dr. T. E. Winecoff at the writer's request, suggests the taxonomic relations of the maker of the tracks.

PARAMPHIBIUS DIDACTYLUS

Willard, n. sp.

Plate 10, figures 1–3

Type specimen.—Paleontological collection, Pennsylvania Topographic and Geologic Survey. (Pl. 10, fig. 1.)

Occurrence and age.—1½ miles east of Lanesboro, Susquehanna County, Pennsylvania; lower Chemung (Cayuta) shale.

Characters of the manus.—The anterior paired appendages, though thought to have been fin-like, are treated as true feet in giving specifications.

Average total length: 11 mm.

Number of "digits": two, each bifurcating; often only the inner digit impressed.

Average lengths of "digits": I,—; II, 10.5 mm.; III, 10 mm.; IV,—; V,—. Actually there is no valid reason for homologizing these structures with one toe any more than another.

Average divarication of "digits": 9°.

Heel: Unknown, probably non-existent.

Palm: At base of each "digit" is an irregularly oval knob about 1 mm. long. These knobs are connected with each other in some examples by an indistinct, transverse ridge.

Other data: Each "digit" arising from a small knob, branches almost immediately into two long, slender, nearly parallel rami that show no joints, claws, nor intervening webs. Some appear to be crossed by fine, transverse lines. The outer ramus is usually slightly shorter than the inner. In juvenile tracks the rami are shorter, more divergent, and Y-shaped.

Character of the pes.—Unlike the manus this was a true foot.

Average total length: 8.5 mm.

Number of digits: five.

Average length of digits: I, 1 mm.; II, 1.1 mm.; III, 1.6 mm.; IV, 2.1 mm.; V, 1.1 mm.

Divarication of digits: 132°.

Heel: Slender, rod-like, extending posteriorly for 4 mm. from edge of sole. Expands distally into flattened end shaped like a diphycercal fish tail, the larger lobe lateral.

Sole: Irregular, 2 mm. diameter, surface uneven.

Other data: Toes spread widely; no claws nor webs seen; joints doubtfully observed; number of phalanges unknown.

General Remarks.—

Average length of stride: 23 mm.

Pace: Individual foot prints opposite to fully alternating (staggered). There is a slight toeing in of the pes.

Average width of track: 22 mm.

Additional marks: Usually none. A single cast of the trail of an adolescent individual shows clearly a median furrow (Pl. 10, fig. 2).

Other data: Comparatively few of the many examples show impressions of the two digits of both fore "feet" usually only one, the median, left a mark.

PARAMPHIBIUS TRIDACTYLUS
Willard, n. sp.

Plate 11, figures 2–3

Type specimen.—Paleontological collection, Pennsylvania Topographic and Geologic Survey. (Pl. 11, fig. 2.)

Occurrence and age.—1½ miles east of Lanesboro, Susquehanna County, Pennsylvania; lower Chemung (Cayuta) shale.

Characters of the manus.—The anterior paired appendages, though thought to have been fin-like, are treated as true feet in giving specifications.

Average total length: 9 mm.

Number of "digits": three, each bifurcating.

Average length of "digits": I,—; II, 6 mm.; III, 8 mm.; IV, 8 mm.; V,—. Actually there is no valid reason for homologizing these structures with one toe any more than another.

Average divarication of "digits": 35°.

Heel: Unknown, probably non-existent.

Palm: No definite data save for small dwellings at base of each "digit" as in *P. didactylus*.

Other data: The track is essentially identical to that described as *P. didactylus* except that it has three, not two "digits." In *P. tridactylus* the bifurcation is less complete, suggesting the younger stages of *P. didactylus*. The rami comprise one-half to one-third the total length of each "digit" and diverge more widely. If this resemblance to a young *P. didactylus* is more than superficial, it may imply through recapitulation that *P. tridactylus* is a collateral ancestor to the former. This would be supported by the probable reduction in number of "digits," remembering that what we are calling "digits" for convenience were probably fin-rays. No claws, webs nor joints were discerned in any example.

Characters of the pes.—Unlike the manus this was a true foot.

Average total length: 5.5 mm.

Number of digits: five.

Average lengths of digits: I, 1.1 mm.; II, 1.1 mm.; III, 1.3 mm.; IV, 1.3 mm.; V, 0.6 mm.

Divarication of digits: 140°.

Heel: As in *P. didactylus*, length 3 mm.

Sole: Nearly circular, 1.6 mm. diameter.

Other data: Impressions, save for minor details, are indistinguishable from *P. didactylus*, which, however, appears to be a little larger.

General remarks.—

Average length of stride: 16 mm.

Pace: More or less alternating (staggered).

Width of track: 15 mm.

Additional marks: None.

Other data: The pes is usually rather weakly impressed or even wanting perhaps implying poorer development than that in *P. didactylus*, a condition agreeing with the suggested greater primitiveness of *P. tridactylus*. Divergence variation between the marks of the rami of the manus in both species indicates that they were very flexible and may have impressed on the bottom as the animal half swam in shallow water with the hind limbs tucked up.

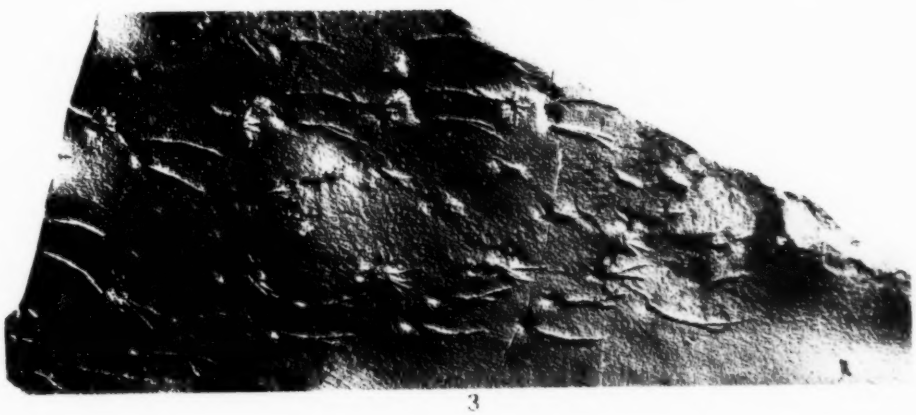
EXPLANATION OF PLATE 11

FIG. 1—View of the track-bearing shales in abandoned quarry near Lanesboro, Pa.

2–3—*Paramphibius tridactylus* Willard, n. sp. 2, The three bifurcating marks left by the "digits" of the fore limb. Type specimens. Note the Y-shaped character of each of these marks as compared with the V-shaped type in *Paramphibius didactylus*. 3, A rather poorly preserved trail in fine, sandy shale, in which the pes impressions are scarcely evident. It is used to illustrate the staggered rather than opposite paces found in some of the trails. All natural size. (p. 48)

1

2



3

Willard, Chemung tracks

DIFFERENTIATING CHARACTERS OF THE TWO SPECIES

Paramphibius didactylus: 2 bifurcating anterior "digits," only one of which may impress; pentadactylous pes.

Paramphibius tridactylus: 3 bifurcating, anterior "digits," all three of which impress; pentadactylous pes.

We observed that the manus of *P. didactylus* may leave only a single bifurcating impression rather than two. These single and double marks were at first thought to have been made by two distinct species, but a slab of extremely fine shale 1.5 mm. thick is the key to this question. On the upper surface is a good trail of *P. didactylus*. When inverted, the slab shows the same trail embossed through, but only one digit (III) registering. No such relation has been discovered between *P. didactylus* and *P. tridactylus*, and they are therefore described as distinct species, a supposition supported by slight differences in the form of the bifurcating marks, as already observed.

DISCUSSION

WHAT WAS PARAMPHIBIUS?

We have described two species of tracks to which the names *Paramphibius didactylus* and *P. tridactylus* have been respectively assigned. Each track consists of two rows of little imprints, and each row is a succession of imprints, every other one of which is alike. That is, two kinds of imprints alternate with one another. Either the maker possessed a series of lateral appendages in which two different sorts alternated throughout and were successively surcharged with remarkable precision in the tracks, or it was a four-footed creature in which the anterior and posterior limbs were, at least superficially, extraordinarily dissimilar.

Several sorts of animals suggest themselves as worthy of consideration as the possible makers of the tracks. Inorganic agencies and plants clearly are not responsible for these marks although such origins have been weighed. It has not been possible to assign the markings to any known animal. We can, however, reduce the range of probabilities if we are able to rule out the invertebrates. Of these only three phyla suggest possibilities, the "worms," molluscs, and arthropods. There is no chance that the trails are those of "worms." These animsls do not stride along on supporting, differentiated limbs. The same is true of the Mollusca. What of the arthropods? Taken alone, the anterior, bifurcating track would almost unhesitatingly be attributed to the clawed leg of an arthropod, but in association with the posterior impressions, the suggestion must be discounted. However, the fact that the appendages were of two different sorts and produced two alternating patterns would not rule out the entire phylum. To be sure, it eliminates all known trilobites, and probably also all of the higher crustaceans of the Upper Devonian, although admittedly little is known of their appendages. Devonian xiphosurans are unknown, but even if they did exist, their trails must have been totally unlike the present specimens, if we may draw inference from those of modern or fossil *Limulus* and its late Paleozoic progenitors. Rare ex-

amples of eurypterids are known from the Chemung of Pennsylvania. The adults of these animals would be too large to produce the tracks, although it is conceivable that the tread is narrow enough for a young individual, a possibility which appeals to us if we recall the anadromous habits assigned to this group in the late Devonian. Three genera of eurypterids, *Eurypterus*, *Stylonurus* and *Pterygotus*, are known to have lived into or beyond Chemung time in eastern North America.[7] The spine-tipped walking legs of *Eurypterus* might have produced scratches, but such marks could not have resembled the bifurcating impressions of *Paramphibius*, nor had *Eurypterus* any organ capable of simulating the five-toed prints common to all of the tracks under consideration. The appendages of *Stylonurus* and *Pterygotus* are even less appropriate than those of *Eurypterus*. Insects and spiders are unknown from the Devonian, and even if present could hardly have possessed appendages to fit these tracks. The limbs of contemporaneous *Scorpionida* are likewise unfitted to have produced the trails, and the diplopods and chilopods have only a long series of undifferentiated appendages. The possibilities of any known arthropod making the tracks seem thus exhausted. Let us turn our attention accordingly to the back-boned animals.

No known vertebrate, fossil or living, could conceivably have made the trails here called *Paramphibius*, but can we postulate an unknown, back-boned animal as responsible for these trials? In such an hypothetical animal the pes left a pentadactylous impression of a little splay foot with sole and heel marks and tiny curved toes, of which III and IV were longest, as in some recent urodeles as well as in certain amphibian tracks from the Carboniferous. Had we only impressions of the hind foot to deal with, we should have little need of further discussions; but the pes tracks alternate with a totally different sort of impression, that of the manus, consisting each of either two or three pairs of long, slender, proximately united depressions which have been referred to as "digits" though admittedly non-homologous. The anterior and posterior relation of the two sorts of tracks is demonstrated in trails in which the pentadactylous prints occasionally overlap slightly the bifurcating prints.

The trails are unlike any known fossil vertebrate tracks from the Mississippian or Pennsylvanian or younger rocks. The only object hitherto described from supposedly nearly contemporaneous strata, and thought to be a vertebrate foot track, is *Thinopus antiquus*, collected by Beecher in Warren County, Pennsylvania. This unique specimen has long excited lively interest, and various concepts of early amphibian evolution have been erected upon its supposed anatomy. Whether it is actually a primitive track that portrays some curious, early adaptation or a pathologic

[7] Clarke, J. M., and Ruedemann, R., The Eurypterida of New York: *New York State Mus., Mem.* 14, p. 431, 1912.

condition, or is an inorganic structure, are questions which still may be raised. At any rate, there is no resemblance between it and the manus of *Paramphibius*, and its likeness to the pes is far less than the resemblance of that mark to the track of a modern frog. Furthermore, *Paramphibius* is considerably the older. *Thinopus* was supposed originally to be late Devonian in age, but the recent admirable studies of the very complicated stratigraphy of the Devonian and Mississippian of northwestern Pennsylvania by Dr. K. E. Caster, of Cornell University, show that it is probably not Devonian at all, but early Mississippian in age (letter of March 24, 1934). So far as known, no older tracks assignable to vertebrates have been identified as such in North America. Hall[8] figured some tiny imprints from the Clinton of New York, some of which show points suggesting toes. However, the number of these ranges from four to eight, and no heel or sole is present. They are doubtfully arranged in parallel rows, and are not staggered. There is no suggestion, through alternating track-type, of differentiation of appendages, but they seem to have been made by a creature equipped with appendages carrying various numbers of terminal bristles. Hall assents to Sir Charles Lyell's opinion that they were made by crustaceans. They were doubtless of arthropod origin and are totally unlike our specimens. The announced discovery of Devonian Stegocephalia in Greenland is significant.[9] If these remains are actually those of a very primitive amphibian with strongly piscene characters, they may well have been contemporaneous with our fossils, although, judging from their reported size, they were much larger animals. We are still waiting final proof of their age. The writer is unaware of any published account of tracks attributed to these animals or to any other contemporaneous vertebrate.

What characters have the Chemung tracks that may lead one to consider them the products of an early but unknown form of backboned animal? The paces are often staggered (Pl. 11, fig. 3), that is, the print of the manus on one side is more or less aligned with that of the pes of the opposite side. In some the paces are opposite (Pl. 10, fig. 2). The fact that the pace thus varies suggests an animal which was passing from a hitching gate to a true, quadrupedal walk, but occasionally lapsed to the older method of progression, especially under exceptional conditions, as noted further on in describing an example of a trail with a tail mark. The important fact of alternation of two kinds of impressions cannot be overemphasized, since it proves the maker of the tracks to have been heteropodous. Furthermore, only one appendage on each side produced five-toed marks and only one made the bifurcating marks, respectively, as contrasted with a

[8] Hall, James, *Paleontology of New York*, volume 2, pp. 35–37, pl. 15, figs. 1–6; pl. 16, figs. 1–4, 1852.

[9] Säve-Söderbergh, G., Preliminary note on Devonian Stegocephalians from East Greenland: *Meddel. om Grønland* (Copenhagen), vol. 94, no. 7, 1932.

succession of alternating kinds of limbs in series. In one trail (Pl. 10, fig. 3) the heel of the right pes is abnormally short, misshapen, and bent. This exceptional imprint repeats in each one of eight paces, which of course alternate with bifurcating marks. In another trail (not figured) a like repetition of a deformity was also noted in a "digit" of the manus. The maker of the track must have had four limbs. It was not merely heteropodous; it was tetrapodous. Since the animal which produced the Upper Devonian trails was thus demonstrably four-legged, it must at that time have been either an amphibian or some unknown form intermediate between the true amphibians and the fishes. What could have been the limb-form of this early track maker? In comparing limbs of vertebrates Kingsley[10] writes:

> These [free appendages] are of two kinds, the paired fins (ichthyopterygia) of the fishes and the legs (chiropterygia) found in all classes of tetrapoda. The former is merely a mechanism for altering the position of the body in the water, and requires a small amount of flexibility, being moved as a whole. The assumption of terrestrial habits necessitates the support of the body above the ground and its propulsion. Hence the chiropterygium must have a firmer skeleton, with at the same time joints for motion and intrinsic muscles to move the parts on each other. The chiropterygium was undoubtedly derived from the fish fin, but the problem of how the change was made has not been solved. Only paleontology can give the answer.

It is recognized that the amphibians are descended from the Devonian Crossopterygii, a group offering the least anatomical difficulties as amphibian progenitors. Lull[11] summarizes this:

> With the crossopterygians . . . the limb is different, having a broad basal lobe containing several bones and a fringe-like expansion so arranged that a much more adequate support is already present, even in the fish stage of evolution. It is particularly in the pectoral fin of the fish *Sauripterus taylori* . . . from the Upper Devonian, that the terrestrial limb is foreshadowed, the shoulder-bones corresponding bone for bone, the single proximal bone of the fin to the humerus, the next two to the radius and ulna, and the remainder, or some of them, to the bones of wrist, palm, and digits. Certain bones have naturally been lost and others added, and the entire fin-rayed portion of the limb abandoned with the relinquishment of the swimming function; but the whole metamorphosis requires no undue tension of the imagination.

The time of this evolution is fixed as late Devonian. The upper Devonian rocks of eastern North America bear evidence of important geographic changes with attendant rapid environmental or climatic alterations. The late Devonian was a time of accelerated adaptation, of rapid organic evolution. Then the change from fish to amphibian occurred. These conditions are demonstrated in the Upper Devonian beds of northeastern Pennsylvania as typically as in many like areas. We recall that the first amphibians were little more than walking fishes, capable of periodic life on land through development of legs and of simple lungs as supplements to gills. These in turn had descended from true fishes probably capable of brief visits to the bare mud flats. Recent examples of land-going fishes are well

[10] Kingsley, J. S., *Outlines of comparative anatomy of vertebrates*, p. 123, 1917.

[11] Lull, R. S., *Organic evolution*, p. 489, 1920.

known among the gobies or mudskippers, while the gurnards have digit-like organs derived from pectoral fin rays and used much as higher vertebrates use their fore feet in crawling or in searching for food. Though devoid of lungs, the gobies are capable of fairly sustained sojourns out of the water, during which intervals the pectoral fins serve in hitching the fish about, often "with the agility of a lizard." The fins are truly ichthyopterygian, with the rays (which may bifurcate) retained. It is a far cry from these specialized, recent teleosts to the late Devonian crossopterygian ganoids, but with like terrestrial adaptation in both groups, similar fin modification to serve the same purpose might occur in each, a not unlikely instance of adaptation of homologous organs to the same use in two distantly related groups at different times. Thus we might suppose that the Devonian stegocephalian ancestor at one time progressed overland by the use of the pectoral fins much as does the modern goby. The ancient fish already possessed in its generalized fin skeleton and rudimentary lungs, structures potential of more specialization, whereas the evolutionary stage of the modern, highly adapted teleost has transcended these primitive requisites.

Published discussions of the origin of amphibians take up only fore limb evolution in any detail. They neglect the posterior pair. Did these evolve simultaneously? Was the pectoral pair developed prior to the other, or were the pelvic fins the first to become legs? Recent amphibian embryology fails to help us materially in this respect. In the Anura the posterior limbs first appear at the surface, but among the Urodela the reverse order is common. However, if a still earlier stage be observed in either group, it seems that both pairs begin to bud almost simultaneously. Among the earliest known skeletal remains of Carboniferous amphibians two pairs of limbs are the rule. Of these the hinder is usually the stronger (larger). The pes commonly has five and the manus four digits, but the feet are otherwise similar. Most of the tracks of early amphibians are pentadactylous, although some show but four fingers. In the known tracks the manus is invariably smaller than the pes.[12] Since the small, four-toed manus is doubtless derived from a five-toed, earlier form of fore foot, it may be looked upon as either a slight degeneration or a specialization, in either case derived from what was a five-toed organ, which may have been larger. In the trails from Susquehanna County it looks as if the manus were the larger, but if the fin rays were removed, the reverse might be the case. With the establishment of more stable terrestrial habits, the fin rays would be dropped. The fact that the hind feet of Paleozoic amphibians are the larger may agree with the condition in *Paramphibius* in implying that the hind foot developed prior to the front. When ambulation was finally established the front foot fur-

[12] Eastman-Zittel, *Text-book of paleontology*, vol. 2, pp. 115, 123, 135, 1902.

ther changed through reduction of digits from five to four, although the primitive five must have been retained in some which represent the ancestors of higher tetrapodous vertebrates.

From the foregoing evidence and the character of the *Paramphibius* tracks we conclude that their maker was an animal which had evolved beyond the generalized crossopterygian ganoid of the late Devonian and had not yet attained a stage as high as that of the most primitive known Carboniferous amphibian. The anterior paired limbs were represented by persistent, fin-like structures, but the posterior had become true walking legs. Thus, the hind limbs, if our interpretations be correct, evolved into feet before the fore limbs. Evidently, for an unknown reason, the manner of earliest terrestrial life of the vertebrates advanced the adaptation of a walking-type of hind leg before it did that of a front leg, with earlier loss of posterior fin rays than of anterior fin rays, and subsequent development of toes.

The diminutive size of the tracks indicates a small animal. Such is in keeping with the recognized tendency to increase in size during racial evolution. Furthermore, the large and more or less specialized Crossopterygii of the Upper Devonian were probably too highly adapted to become the ancestors of the amphibians. Rather, we should look for some small, generalized member of the group as the progenitor of the earliest Stegocephalia.[13]

[13] Romer, A. S., *Vertebrate paleontology*, p. 104, 1933.

ENVIRONMENT AND HABITS

What of the environment and habits of *Paramphibius?* The fossils associated with the tracks are, so far as we know, all nonmarine. The stratigraphic succession implies a gradual disappearance of marine conditions with withdrawal of the sea westward from northeastern Susquehanna County in early to middle Chemung time. The recurrent marine fossils below the foot-track shales and rapid changes in type of sediment point to conditions of instability. An estuarine environment might be postulated, since the toxic effects of brackish water upon ancient amphibians cannot be established. Possibly we deal here with deposits in a fresh-water body behind a bay bar. The local paleogeography shows[14] a Chemung deltal lobe building westward into the interior sea and changing the environment of northeastern Pennsylvania from marine to brackish or fresh-water and eventually to dry land. Estuaries, lagoons, ponds and streams might therefore occur. The fineness of much of the foot-track shale and its even bedding (ripple marks are scarce, rain prints and mud cracks unknown) argue for deposition in quiet water. Many casts of vertical plant stems suggest a vegetation-filled swamp, a suggestion substantiated by the occurrence of at least one thin coaly layer. *Paramphibius* dwelt partly on land and partly in shallow, probably fresh water.

We have cited the evidence that

[14] Willard, Bradford, Early Chemung shore line in Pennsylvania: *Geol. Soc. Am. Bull.*, vol. 45, pp. 897–908, 1934.

Paramphibius was a tetrapod. What was its method of locomotion? Modern "walking fish" use the pectoral fins as organs of propulsion over the land, but *Paramphibius* had advanced beyond such a stage. That it sometimes partly reverted from a truly walking to a hitching gate is shown by some few trails in which the paces are opposite. One specimen of an immature *Paramphibius didactylus* clearly shows a tail mark (Pl. 10, fig. 2). This, we believe, implies that that appendage was used only occasionally, presumably under unusual circumstances. This particular trail was made in fine, soft mud. In the straight part of this trail a narrow groove is found equidistant between the rows of foot prints; where the trail is curved, this mark is deflected to the outer side. The tail groove shows a slightly nodose or beaded character as if pressure had been alternately applied and relieved, the nodes lying approximately opposite intervals between the paces, which are here opposite, not staggered. The steps themselves are close together, crowded and sometimes overlap. In the curved part of the trail the toes on the inside track have dragged sidewise, and the mud at the opposite margin is heaped up slightly as if the body had slid laterally a trifle. Observed examples of mud flows preserved in the shale are not rare. The fact that the mud flowed implies occasional inclined surfaces. Evidently, a small individual tried to climb a soft mud slope or bank, perhaps out of water. At first it slipped sidewise as it pursued a course diagonal to the grade. In so doing it "skidded" down hill a few millimeters, the tail braced and the little toes scratching and scrambling for a foothold. Then, turning more directly up hill, it pushed itself along by a series of jerks in which the feet were moved together like oars, not alternately as a quadruped walks. The tail, pressed into the mud whenever the feet were raised and brought forward, acted as a brace to prevent slipping backward. Faint, diagonal marks between the tail mark and foot prints may have been made by ventral armor. Such a protective covering must have been valuable to an animal which dragged the ventral surface over the ground when crawling out of water. One or two other trails out of scores show tail impressions, but are all poorly preserved and give no additional information. In still others the foot prints are crowded closely together, but no median marks are seen. These are, however, poorly preserved in sandier shale that may have failed to record tail marks.

Why are there so few tail marks? Most of the trails are of larger and therefore more mature animals than the skidding individual described. Possibly the adult walked with the body and tail clear of the ground, a supposition which seems questionable in an animal whose trail is rather wide for the size of the foot prints. Probably all individuals dragged the tail more or less on land, but left no such mark when in the water where *Paramphibius* might half swim, half wade at or below the surface with the

feet just impressing. An analogous mode of progress has been observed by the author in axolotl, the permanently larval form of the North American tiger salamander, *Amblystoma tigrinum*, found in the region of Mexico City. This animal may be seen to walk under water on the bottom with the body and tail out of contact with the substratum, only the feet touching. The fact that in *P. didactylus* sometimes only a monodactyl track of the manus (Pl. 10, fig. 3) was left substantiates this view in implying different degrees of pressure applied in walking. These marks were, however, made in soft mud. In certain fine-grained sandstone slabs impressions of the pes are numerous, but the manus is practically lacking. It is incredible that we are dealing with an animal which assumed on occasion a bipedal gate. The stage of evolution is too early, although such an explanation of this anomaly would be welcome. Doubtless the correct interpretation is that the more delicate fin rays of the front limbs failed to impress where the sturdier hind feet left tracks, or that the fin-like front feet were being used as true fins while the foot-like hind limbs made contact with the bottom. A few examples of multiple trails were found. Here two or more individuals followed the same route, the successive foot tracks being superimposed upon preceding ones. As the trails cross and recross innumerably such a chance succession is quite possible.

If our observations and deductions be true, *Paramphibius* spent much of its life in shallow water, where its habits may have closely approximated those of the modern axolotl. Where, however, that salamander is degenerate, has reverted toward the ancestral, gilled stage, and cannot survive on land because of nondevelopment of lungs, being neotenous, *Paramphibius* was progressive and came on land occasionally to crawl about, somewhat after the manner of the living, land-going fishes, but with the important differences that the hind limbs were adapted to terrestrial life and typically evolved, and the simple lungs were functional. It is noteworthy that the hitching gait appears to have been preferred on land, and that which produced staggered paces, a definite striding gate, in bottom-walking. Such conditions seem paradoxical, but nevertheless suggest that the present pace of terrestrial vertebrates developed in the water.

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A MARSUPIAL FROM THE FLORISSANT BEDS (TERTIARY) OF COLORADO[1]

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ABSTRACT

The Florissant beds have yielded remains of fish and birds, but no identifiable mammal remains have hitherto been recorded. A small marsupial, *Peratherium* near *P. huntii* (Cope), is here described and interpreted as favoring an assignment to the Oligocene or lower Miocene rather than the upper Miocene, now widely accepted.

In 1929 the U. S. National Museum purchased from Mr. George F. Sternberg the skeletal remains of a small mammal collected by him in the Florissant beds at a locality a short distance southwest of the town of Florissant, Colorado. Hitherto no identifiable mammalian remains have been recorded from these beds, although a few birds and fish have been found. Early descriptions of the fragmentary fish were made by Cope (1874, 1875, 1878, and 1884) and by Osborn, Scott and Speir (1878). Later accounts of the fish are principally those of Cockerell (1908, 1913, and 1914). Reports on the bird remains have been made by Allen (1878), Cope (1881, and 1884), Shufeldt (1913 and 1917) and Wetmore (1925, 1928, and 1929). The fossil vertebrates now known are as follows:

Fossil Vertebrates of the Florissant Beds

Pisces
- Holostei
  - *Amia scutata* Cope
  - *Amia dictyocephala* Cope
- Ostariophysi
  - *Rhineastes pectinatus* Cope
  - *Amyzon commune* Cope
  - *Amyzon pandatum* Cope
  - *Amyzon fusiforme* Cope
  - *Amyzon* sp. indet.
- Xenarchi
  - *Trichophanes foliarum* Cope
  - *Trichophanes copei* Osborn, Scott and Speir

Aves
- Charadriformes
  - *Charadrius sheppardianus* Cope
- Passeriformes
  - *Palaeospiza bella* Allen
- Incertae sedis
  - *Fontinalis pristina* Lesquereux

Mammalia
- Marsupialia
  - *Peratherium* near *P. huntii* (Cope)

The Florissant beds are well known for the great abundance and variety of remarkably well preserved fossil insects, spiders and plants which they have produced. The most noteworthy studies of the insects and spiders were those made by Samuel H. Scudder and by Cockerell. The more general investigations of the flora from these beds include those of Lesquereux, Kirchner, Cockerell, and Knowlton.

[1] Manuscript received October 30, 1934.

SYSTEMATIC DESCRIPTION

PERATHERIUM near P. HUNTII (Cope)

Plate 12

The mammal specimen discovered by Mr. Sternberg apparently represents the extinct genus *Peratherium*, and is unique in exhibiting so much of the skeleton. The specimen is exposed on a shale slab, most of the bones being represented by impressions. The skull and right ramus of mandible are present, although the skull is considerably crushed. Only the lower dentition is preserved. Much of the vertebral column and ribs are represented only by impressions. Part of one forelimb and portions of both hind limbs are seen with flakes of bone adhering in places to the natural mould.

Peratherium is a didelphid resembling the small murine opossum *Marmosa*, now living in southern Mexico, Central and South America. Among the living species the Florissant specimen is found to correspond most closely in size to the small *Marmosa microtarsus* of southern Brazil. Comparisons made between the fossil and a skeleton of *M. microtarsus* in the National Museum collections of Recent mammals show a certain degree of similarity between the two forms. Several rather apparent differences are observed, however, notwithstanding the crushed condition of the fossil.

The skull.—Relative proportions of the fossil skull cannot be obtained with any degree of accuracy, although its general size and shape and the characters of the lower dentition can be ascertained. In length the skull is about equal to that of *Marmosa microtarsus*. The orbit does not appear to be placed so far forward as in *Marmosa*, and the anterior and superior margin appears to be more sharply outstanding, apparently more so than in such forms as *M. canescens* of Mexico. The prominence of the orbital margin is very noticeable, but this may have been affected in part by distortion. The brain case is well inflated, the width at the postorbital constriction being very much greater than in *M. microtarsus* and relatively greater than in larger species of *Marmosa*. There is no indication of a sagittal crest such as exists in *Didelphis virginiana*. The slightly developed and widely separated temporal ridges extend a short distance posterior to the rather prominent postorbital processes.

Dentition.—The lower dentition has the formula I_{1-4}, C, P_{1-3} and M_{1-4} as in *Marmosa* and related forms. The teeth are in a continuous series, closely placed but not crowded. The procumbent incisors with the canine occupy a somewhat larger space than in the Recent mandible measured. These teeth appear to be moderately large, although the tip or crown portion of each is missing. The premolar series following directly behind the canine is distinctly shorter than in the specimen of *M. microtarsus*, and the second premolar appears to be slightly smaller than the third. In some specimens of *Marmosa elegans* the second premolar below does not appear to be more elevated than P_3, although in many specimens observed in other species this tooth stands above P_3. The molar series is slightly longer than that in the specimen of *M. microtarsus* measured. Although there appears to be a certain amount of variation in the length of the tooth row within species of *Marmosa*, the relative shortness of the premolar series as com-

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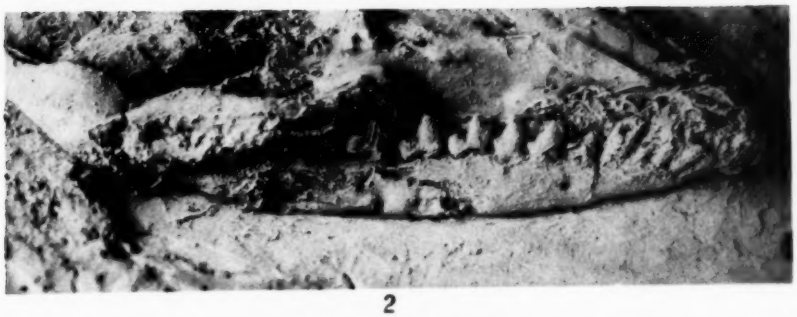
EXPLANATION OF PLATE 12

FIGS. 1–3—*Peratherium* near *P. huntii* (Cope), partially crushed skeleton on a shale slab, U. S. N. M. cat. no. 11955, from the Florissant lake deposits SW. of Florissant, Colorado. 1, Skeleton as exposed in plane of stratification, natural size; 2, lateral view of mandible and lower dentition, ×4; 3, skull and mandible, ×4. Photographs by C. E. Resser. (p. 58)

1



2

3

Gazin, Marsupial from Florissant

pared with the length of the molars may be considered as distinctive. The structure of the individual teeth in the molar series does not differ greatly from that seen in recent specimens of *Marmosa*, but a few characters observed appear to be of importance. In the trigonid of M_1 the paraconid is nearly as high as the protoconid and separated from it by only a slight notch. These two cusps are closer together than in succeeding teeth, and the antero-external surface or shear is directed somewhat more antero-posteriorly. Moreover, the antero-external cingulum rises anteriorly more steeply toward the paraconid. In *Marmosa* the paraconid of M_1 is much lower, more lingually placed, and better separated from the protoconid, and the cingulum does not ascend so steeply toward the paraconid. In the fossil the posterior wall of the trigonid, as seen in M_1 and M_2, is directed backward lingually more than in *Marmosa;* the lingual cusp of the talonid appears high and less markedly separated from the metaconid; and the hypoconid is separated from the protoconid by a deeper notch than in *Marmosa*.

Vertebral column and limbs.—The vertebral column is about the length of that in *M. microtarsus* although there is some evidence from the impression that the combined cervical and dorsal portion may be somewhat longer than in the modern skeleton used in this comparison. In the fore limb the humerus is nearly as long as in *M. microtarsus*, but the radius and ulna are distinctly shorter than in this recent skeleton. Furthermore, the metacarpals are considerably longer in the fossil and show greater size differentiation than is the case in *M. microtarsus*. In a comparison of foot bones it should be noted that *M. microtarsus*, as observed by Tate,[2] is characterized by small feet, however, the relatively long metacarpals in the fossil manus distinguish the Florissant form even when comparisons are made with the available skeletons of other species of *Marmosa* in the National Museum. In the hind quarters the innominate bone is slightly longer from the proximal end of the ilium to the ischial tuberosity, but apparently narrower as measured from the superior margin of the ischium to the ischial symphysis. The femur is only slightly shorter than in

[2] Tate, G. H. H., *Am. Mus. Nat. Hist., Bull.*, vol. 66, art. 1, p. 31, 1933.

MEASUREMENTS OF SKELETON

	Peratherium cf. *huntii* U. S.-N. M. cat. no. 11955	*Marmosa microtarsus guahybae* U. S.-N. M. (Div. Mammals) cat. no. 236677
	mm.	mm.
Length of skull	26*	26.0
Distance from anterior margin of orbit to anterior end of skull	11*	9.5
Depth of lower jaw below M_1	2*	2.0
Length of lower dentition, I_1-M_4 inclusive	12.0	11.4
I_1 to C inclusive	2.9	2.3
Length of lower premolar-molar series, P_1-M_4 inclusive	8.8	8.9
Length of lower premolar series, P_1-P_3 inclusive	3.0	3.3
Length of lower molar series, M_1-M_4 inclusive	5.8	5.6
Length of humerus	13.0	14.0
Length of radius	12.5	15.1
Length of ulna	14.7	17.4
Width across radius and ulna distally	2*	1.9
Length of metacarpal I	2.0	1.9
Length of metacarpal II	3.7	3.0
Length of metacarpal III	4.0	3.2
Length of metacarpal IV	3.7	3.0
Length of metacarpal V	2.3	2.1
Distance from proximal end of ilium to tuberosity of ischium	16.8	16.1
Distance from superior margin of tuberosity of ischium to ischial symphysis	5.3	5.8
Length of femur	16.0*	16.4
Length of tibia	17.3	20.6
Length of fibula	17.0*	20.5

* Approximate.

M. microtarsus, though the tibia and fibula are appreciably shorter, being comparable in this respect with the relatively short fore-arm of the anterior limb. Neither hind foot is sufficiently well preserved to permit comparisons, although a portion of both right and left tarsus can be seen.

Comparisons.—The Florissant form corresponds closely in size to *Peratherium huntii* (Cope),[3] from the Cedar Creek beds of northeastern Colorado, to which species it may belong. Of the several forms described from the White River beds in Colorado, *P. huntii* is the smallest, and is further characterized by an uninterrupted premolar series. Comparisons between the Florissant specimen and *P. huntii* are limited to characters of the mandible and lower dentition, as the species is known only on mandible portions, and specific identifications are somewhat unsatisfactory. The mandible portion indicated as the type of *P. huntii* (Am. Mus. cat. no. 5266) includes the three posterior molars, which exhibit a high trigonid with a well developed metaconid. The entoconid in this specimen is not so large and is much more clearly separated from the metaconid than in the Florissant specimen. Of the several Cedar Creek jaws, no. 5266 comes nearest in size to the Florissant form. A somewhat smaller specimen (Am. Mus. cat. no. 5257), designated as a cotype, exhibits P_2 and the first two molars. In the molars of no. 5257 the entoconid is rather prominent and less sharply separated from the metaconid than in the molars of the type; and these two cusps are more nearly equal in size in no. 5257 then in the type, as shown in the second molar, which is included in both specimens. No. 5257 may represent a distinct species. The development of the entoconid and its proximity to the metaconid in no. 5257 is an approach to the condition seen in the Florissant specimen, but the paraconid of M_1 in no. 5257 is much lower with respect to the protoconid, and the length of the premolar series was considerably shorter, as indicated by the alveoli. A third mandible specimen of *P. huntii* (Am. Mus. cat. no. 5266), originally the type of *Herpetotherium stevensonii*, resembles the type of *P. huntii*, but is slightly smaller, shows less disparity in size between the metaconid and entoconid, and has the talonid of M_4 much narrower than in the type.

Peratherium titanelix Matthew,[4] from the *Titanotherium* beds at Pipestone Springs, Montana, is slightly smaller than the Florissant form, but falls within the range of size for specimens of *P. huntii*. The alveoli for the lower premolars in the Montana form are more crowded and the series relatively a little shorter than in the Florissant specimen, although the anterior portion of the lower jaw appears nearly as deep.

Peratherium merriami Stock and Furlong,[5] from the Upper Oligocene or Lower Miocene John Day beds of eastern Oregon, is the only known species occurring in deposits of later age than White River. This form is apparently much larger than *P. huntii*.

AGE OF THE FLORISSANT BEDS

The age of the Florissant beds has been variously regarded as anywhere from Eocene to Pliocene. As the beds are isolated from other Tertiary deposits by crystalline rocks, age determinations have depended largely upon interpretations of the known fossils. A. C. Peale in 1874 regarded

[3] Cope, E. D., *U.S. Geol. Geog. Surv. Terr., Ann. Rept., 1873*, p. 466–467, 1874.

[4] Matthew, W. D., *Am. Mus. Nat. Hist., Bull.*, vol. 19, p. 202, 1903.

[5] Stock, Chester, and Furlong, E. L., *Univ. Calif. Publ., Bull Dept. Geol. Sci.*, vol. 13, pp. 311–317, 1922.

them as possibly of Pliocene age.[6] Cope in 1874 and 1875, in comparing the fish from these beds with those of the Green River shales, regarded them as somewhat younger than the Green River stage. In 1879, he considered the age to be later Eocene or early Miocene.[7] Lesquereux[8] in 1874 believed the plant remains to be late Miocene, but later,[9] upon examining a larger collection, regarded the Florissant beds, which he referred to the Green River group, as Oligocene in age. Scudder[10] in 1882, in summarizing the conclusions of Cope and Lesquereux, placed the beds in or near the Oligocene. However, in 1906, Cockerell[11] revived the late Miocene age determination, and in this was later supported by Knowlton[12] and by Berry.[13]

The occurrence of the genus *Peratherium* in the Florissant beds, a fact established by the present find, is suggestive of a lower Tertiary age, since marsupials are not known in the Tertiary of North America after John Day time. This cannot be regarded as more than negative evidence, but the absence of the group is becoming increasingly significant as knowledge of North American upper Miocene and Pliocene faunas increases.

[6] Peale, A. C., *U.S. Geol. Geog. Survey Terr., Ann. Rept., 1873*, p. 210, 1874.

[7] Oligocene not recognized.

[8] Peale, A. C., *op. cit.*, p. 210.

[9] Lesquereux, Leo, *U.S. Geol. Survey Terr., Rept.*, vol. 8, pp. xi, 129, 1883.

[10] Scudder, S. H., *U.S. Geol. Geog. Survey Terr., Bull.*, vol. 6, pp. 299–300, 1882.

[11] Cockerell, T. D. A., *Univ. Colorado Studies*, vol. 3, p. 160, 1906; also *Am. Naturalist*, vol. 44, pp. 31–47, 1910.

[12] Knowlton, F. H., *U.S. Nat. Mus., Proc.*, vol. 51, p. 244, 1917.

[13] Berry, E. W., *U.S. Geol. Survey, Prof. Paper* 154, p. 234, 1929.

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VIEWPOINTS AND OBJECTS OF PALEOECOLOGY[1]

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ABSTRACT

Paleoecology is essentially concerned with organisms or communities of organisms in relation to their environments. The subject matter of ecology may be divided into autecology and synecology, or individual and associational ecology. Paleoecology may well form a third division because of peculiarities resulting from the fact that the organisms dealt with are fossils. The viewpoints of paleoecology are biologic in character; one is physiologic, the other is sociologic. The first seeks to clothe a fossil with life, the second to consider the communities which composed a a flora or fauna. The peculiarities of paleoecology are that it must be chiefly descriptive, it must lay its emphasis on autecology and its historical scope. Paleoecology must deal largely with sessile organisms, whose response structurally to environmental changes is large. In these there is need to distinguish somatic changes from fixed hereditary characters. Adaptations must be used with care and reinforced by corroborative evidence. They are not necessarily valuable data of paleoecology. Autecology will yield sedimentologic data, functional data, and morphologic data. Synecology involves the synthesis of autecologic data and the statistical study of fossil communities. In these the limitations of fossilization enters. Paleoecology combines biologic viewpoints and data with paleontologic and geologic materials and methods. It organizes on a biologic basis facts of taxonomy, stratigraphic paleontology, stratigraphy, and sedimentology. It is, however, primarily concerned with the sociology of fossil organisms, and any narrower concept will hamper its development and its usefulness.

INTRODUCTION

Definitions of ecology.—As its name indicates, paleoecology is the ecology of ancient or fossil plants and animals. Like such branches of paleontology as taxonomy and evolution, it applies to organisms of the geologic past viewpoints, objects and even disciplines developed from and for living things. Thus, though modifications and extensions meet special needs, its basic viewpoints and objectives are identical with or derived from those of its modern predecessor. To say what paleoecology is and what it seeks, we first must define ecology.

Chapman (1931, pp. 1–3) has briefly traced the history of ecology. As "bionomics" its organic aspects appear in the *Histoire naturelle, générale et particulière* of the much misunderstood Buffon. As "ethology," Isidore Geoffroy Saint-Hilaire proposed to make it the subject of a volume on "the relations of the organism within the family and the society, in the aggregate and in the community." This statement was made in 1859, but the promised volume was not published. Ten years later, Haeckel (1869, p. 365) used ecology, or *Oekologie*, to include the "relationship of the animal to its inorganic as well as

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its organic environment, especially its friendly or hostile relations with those animals or plants with which it comes in contact."[2]

This definition seems to underlie most of those given today. A survey of many papers and books shows agreement on these points: (1) Ecology is that branch of biology which deals with the relationships of organisms to their surroundings. (2) It is concerned with (a) whole organisms, (b) groups or communities of organisms, and (c) with both inorganic and organic factors of the environment or parts thereof.

There are some, however, who think that relationships should be made more clear, scope more specifically stated. So we find Shelford (1913, p. 1) saying that "ecology is that branch of general physiology which deals with the organism as a whole, with its general life processes, as distinguished from the more special physiology of organs, and which also considers the organism in particular reference to its usual environment." In a more recent work (1929, p. 1) he says that one division of biology is bioecology, which is the sociology of organisms. The definition is simple and inclusive, though it gives sociology a wider scope than is claimed for it by most sociologists. For this reason a more explicit definition may be preferred; if physiologic implications are kept in mind, our composite one may suffice.

Subject matter of ecology.—We have seen that ecology is concerned with organisms and communities of organisms in relation to their environments. This statement demands amplification, for an animal or plant is various things to those who consider it variously. To the taxonomist, it may be a series of described characters; to the anatomist, a system of organs; to the stratigrapher, an index of geologic age. To the ecologist, it may be any or all of these, but it first is a living thing—an agent of chemical and physical change maintaining its own identity. Hence we find ecologists framing such definitions as these:

An organism is a system in dynamic equilibrium.

An organism is a coördinated, individualized system of activities.

An organism is a physico-chemical mechanism capable of self-maintenance and reproduction.

An organism is a complex system of activities taking place under specific conditions in a special, complex body. It maintains itself by taking matter and energy from the environment, to which it returns matter and energy as waste.

Such is the concept of organism on which ecology is based. Its subject has a few common needs: water, food, freedom from harmful dirt and waste,

[2] "Unter Oekologie verstehen wir die Lehre von der Oekonomie, von dem Haushalt der thierischen Organismen. Diese hat die gesammten Beziehungen des Thieres sowohl zu seiner anorganischen, als zu seiner organischen Umgebung zu untersuchen, vor allen die freundlichen und feindlichen Beziehungen zu denjenigen Thieren und Pflanzen, mit denen es in direkte oder indirekte Berührung kommt. . . . Diese Oekologie (oft auch unpassend als Biologie in engsten Sinne bezeichnet) bildete bisher den Hauptbestandstheil der sogennanten 'Naturgeschichte' in dem gewöhnlichen Sinne des Wortes."

safety from attack, conditions for propagation, and (except in special cases) air. In securing these it lives near other organisms; through proximity, special function or need it enters societies which generally are complex. To paraphrase our definitions of organism, such societies are coöordinated systems of living things capable of self-maintenance under specific or limited conditions.

Among the conditions thus limited are some provided by the organisms themselves. Societies form environments, such as those of forests for animals dwelling in them, while some individual types or species exert controlling influence on others. Yet the most widespread society (community) is small when compared with oceans, continents, or the earth, on whose outer parts it depends. Environments may be organic; environment is essentially physical. In the restricted parts of it called habitats, the environment may involve trees, rockweeds, or coral heads; in the sea as a whole it becomes an affair of water, dissolved gases, and minerals. As the earth, and even the universe, its essentials have been resolved by Henderson (1913) into carbon dioxide and water. Others would add nitrogen, sunlight and radiant heat. The point is not which may be right; it is the extent to which the environment may be reduced first to physiographic and meteorologic factors, and finally to those of physics and chemistry.

Divisions of ecology.—On another plane, that of emphasis and methods, the subject matter of ecology may be divided into autecology and synecology, or individual and associational ecology. The first terms are those of Schröter (1896, 1902); the second, those of Adams (1913). Since Schröter's terms enjoy priority and wide usage, they may be adopted by paleontologists.

Not, however, without noting that some ecologists hold them unnecessary. Thus we find Shelford (1929, p. 2) saying:

> At the present time there is no need and little justification for the term "autecology" . . . or . . . for the use of the term ecology referring to particular species as very commonly construed. Ecology is a science of communities. A study of the relations of a single species to the environment conceived without reference to communities and, in the end, unrelated to natural phenomena of its habitat and community associated is not properly included in the field of ecology.

The point does not seem well taken. Even if the study of a single species meets Shelford's requirements, it is the study of that species not a community. Frequently, also, the paleontologist makes that species, or a few of its associates, serve him in place of a vanished community. Historical problems frequently call for studies of the habits of species, genera or even larger groups, in which the inorganic environment rather than the community furnishes the essential background. Even when the community is considered, it may be of tertiary significance.

Such studies seem properly grouped under the heading of autecology. They deal with physical factors of the environment in relation to se-

lected taxonomic groups, and with those complex qualities of the organism summed up in the phrase "biotic potential." Much of their concern is physiologic, though as communities enter in the role of backgrounds they assume sociologic scope.

Synecology, on the other hand, is concerned with the description and distribution of population systems and their interpretation on a basis of biotic potential and environmental fitness or resistance. Descriptive ecology may confine itself to the present, but in the field of distribution it finds strong links with the past through biogeography (distribution of communities in space) and succession (their distribution in time). Both, like physiology, are dynamic rather than analytic or descriptive.

Despite these synecologic links with the past, we must add to Schröter's two a third division. Paleoecology may be only the autecology and synecology of fossil plants and animals, but the very fact that they are fossils introduces problems, implications and methods so distinctive that they demand a category of their own. For reasons to be stated in the section on adaptations, neither "ethologic paleontology" (Dollo) nor "paleobiology" (Abel, Dacqué) seems suitable. Awkward though "paleoecology" is, it seems the best term available.

It is not needful to mention here the taxonomic, stratigraphic, and sedimentologic links which join paleoecology with the earth sciences. They are those which similarly affect paleontology, with added emphasis on sediments, as Twenhofel and his collaborators (1932) have implied.

VIEWPOINTS OF PALEOECOLOGY

Despite its geologic affiliations, paleoecology rests on biologic viewpoints, since it considers fossils as organisms, not as constituents of sediments. Of these biologic viewpoints, two may be specified as essential. Though they have been mentioned in connection with ecology *sensu stricto*, they may be restated and developed paleontologically here.

The physiologic viewpoint.—In common with its sister subscience, paleoecology views organisms as complete entities living and functioning in environments. This viewpoint is physiologic, since it considers functions and processes, however much actual study may be hampered by the fact that the animals and plants are dead and preserved or recorded in rocks. Paleoecology seeks to clothe the fossil not merely with the flesh, but with the needs, abilities and functions of life.

Perhaps this is best shown by two contrasting definitions of a fossil. The first is that given his students by the late Doctor Stuart Weller, a taxonomist and stratigrapher. The second is phrased to make explicit for fossils the concept of organisms held by ecologists such as Pearse and physiologists such as Child.

1. A fossil is the remains, impression, or trace of an animal or plant that lived during past geologic time, buried in rocks of the earth's "crust."

2. A fossil is the direct record of a physico-chemical mechanism ca-

pable, under specific or limited conditions, of a complex system of activities resulting in survival, self-maintenance and reproduction. This record consists of traces, impressions or partial remains buried in rocks of geologic age.

It is not contended that the second definition is either wieldy or essential to daily work. But until the scope of paleoecology is more generally admitted and its objects more generally sought, the essentials of this definition will require frequent attention and emphasis.

The sociologic viewpoint.—Fossil organisms, like their modern descendants, formed interrelated societies. These societies, even more than the organisms themselves, are the concern of paleoecology. In so far as they rested upon functional characters and environmental influences, those societies were physiologic. Yet full consideration of them transcends even general physiology. In concerning itself with constituents, numbers and balance in population systems, paleoecology reaches the plane of general sociology—the sociology of all organisms.

Paleontology frequently deals with those large, enduring societies known as faunas and floras. Typically, it treats them by means of lists of species and subspecies, or by descriptions of these taxonomic units. Sociology is approached only when the lists are restricted to minor stratigraphic units such as zonules, and are supplemented by data on relative abundance and areal variation in distribution.

To reflect adequately the sociologic viewpoint, faunas or floras must be resolved into their constituent communities, to be described in at least the detail provided by Davies (1921) for the Westphalian plants of Wales, and by Pearse (1913) for the modern littoral fauna of Nahant. This detail specially concerns the relationships between organism and organism and between organisms and environment—matters generally ignored in taxonomic studies.

It is quite possible, also, for sociologic (synecologic) studies to accomplish their purpose without listing all or even most of the organisms in the societies with which they deal. Thus Shelford and Towler (1925) limit their lists to the dominants in animal communities of Puget Sound, with occasional mention of subdominants. A study of the Hamilton communities (cenoses) of western New York, or of the stromatoporoid biostromes of Iowa might well adopt such a plan. Its chief virtue is simplification of relationships; its most serious defect is that such simplification may omit relationships of considerable importance because they do not involve obvious dominants and subdominants. Thus the Shelford-Towler lists fail to indicate the importance of bryozoans, hydroids and annelids in several of their cenoses, or associations.

PECULIARITIES OF PALEOECOLOGY

When we compare paleoecology with the ecology of modern organisms, we find certain peculiarities which derive from the nature of its

materials. They determine secondary viewpoints and many immediate objects; they involve limitations that ecologists proper often overlook. For these reasons it seems well to detail them here.

Emphasis on description.—Modern ecology relies largely upon quantitative analyses of communities and experimental studies of environments and reactions to it. The former may be applied to the fossils of suitable formations as Fenton and Fenton (1928, pp. 12–13) and Belanski (in still unpublished work) have shown; yet there are many cases in which quantitative study is impracticable. In such instances, more general methods may be employed, resulting in descriptions comparable to those of Pearse (1913), Shelford and Towler (1925) and Davies (1921). In view of uncertainty as to the length of time represented by any given stratum that may be chosen for ecologic study, such inexact descriptions are less defective than they at first seem.

Experiment, except in the related field of sedimentation, and upon living organisms used for comparison, naturally lies beyond the scope of paleoecology. Since biologic experiment calls for its own special equipment and technique, the majority of paleoecologists will find themselves forced to adapt the results of biologic work to their own problems—again on an essentially descriptive basis. This means that most autecologic studies of fossils also must be descriptive, of the sort which when applied to living organisms, is generally termed natural history.

Emphasis on autecology.—Though the sociologic viewpoint has been stressed as one essential to paleoecology, limitations imposed by preservation often place emphasis on autecology. Very commonly, traces, often of one or a few species, are the chief data from which the associations of sandy littoral zones must be restored; while material is similarly limited to shells or corals in the case of some limestones. Here, though viewpoint and objectives may be synecologic, the actual procedure of study stresses individual groups or species.

The importance of such groups in geologic history also directs attention to their ecology. It may, for instance, be highly desirable to know the environmental and communal relationships of crinoids, of *Atrypa*, or of calcareous algae through periods and even eras. In such cases the method of work is autecologic, even though the group considered is much larger than the species, for which Schröter proposed his term.

Emphasis on autecology may diminish as more formations and fossils are studied. For the present, it affords an approach to paleoecology that is more available and of more immediate utility than that provided by synecology. Nor is effort given it lost to the latter field, since much of the synecology of fossils must be a synthesis of autecologic data.

Emphasis on history.—Aside from the nature of its records, paleoecology differs from modern ecology chiefly in its historical scope. The ecologist deals with the succession of societies and environments from year to year

or decade to decade; at most, he extends his attention to those of Pleistocene and later time. Now that Proterozoic faunas (David, 1928) and floras are becoming well known, the paleoecologist finds the societies of some six hundred million years awaiting his attention. One of his chief tasks is to deal with their succession, modification, and migration during this long period.

Even the detailed paleoecologic study has a historical scope far greater than that of most ecologic work. The bioherms (reefs) of Silurian age described by Cumings and Shrock (1928), algal biostromes in the Belt series, or a single stratum of fossiliferous Richmondian shale, represents a period of time greater than that involved in a climax forest, a tide pool, or a laminarian colony. If ignored, this distinction may produce error; if made the basis of comparative study, it furnishes the ground for seral studies of importance to both ecology and biogeography.

Terminology.—In general, paleoecology may adopt standard ecologic terms. There are cases, however, in which others may be introduced to meet the limitations of geologic preservation (Fenton and Fenton, 1928, pp. 9–15), and two others in which ecologic terms may not be applied to fossils without confusion.

"Stratum" and "formation" had established geologic meanings long before they were adopted by ecologists. By the latter, there use has been far from uniform and has involved synonyms. The "stratum" of Shelford (1913) seems identical with the "layer society" of Nichols (1923, pp. 19, 174), while Klugh (1923, p. 369) has shown that the ecologic term "formation" is best clarified by being dropped.

As another paper (Fenton and Fenton, 1935b) shows, paleoecologic work does not require a complex nomenclature, and may suffer confusion from it. The simple "common system" proposed by Klugh seems to meet most practical needs, though individuals doubtless will find instances where it must be modified to fit their materials.

STRUCTURE IN PALEOECOLOGY

Response.—Because they commonly are well suited to preservation, paleoecology deals largely with sessile organisms. As Shelford (1914) has shown, such organisms show their most striking responses to environmental influence on morphologic or structural change. In many cases, growth forms of plants are closely paralleled by those of sessile animals.

Such responses, as well as those of activity, are important data of paleoecology. In the past, however, few efforts have been made to distinguish somatic responses from fixed hereditary characters of ecologic significance. Many paleontologists, indeed, seem to assume that this distinction does not exist. Thus we find Dunbar (1924) and Berry (1928) following Hyatt (1894) in merging somatically acquired characters with hereditary ones in the evolution of cephalopods, while Thomas (1925?) described a species of stromatoporoid whose

only distinguishing character was large colonial size.

There is need for critical studies to determine true morphologic responses and link them with their environmental causes. For the purposes of paleoecology, it is not important to inquire whether these responses become hereditary or not. Nor is the problem one of fitness or adaptation; it involved physiologic responses regardless of their utility, and will be confused if the latter point intrudes.

The problem admittedly is not simple, for responses occurring through successive generations will assume the guise of specific or subspecific characters. There also is need for much more detailed stratigraphic data than generally have been collected for paleontologic purposes, and for comparative studies of modern organisms. At best, the case is one in which analogy often must be assumed to signify homology, the assumption being justified or disproved by the frequency or infrequency of corroborative cases.

Adaptation, fitness.—"In animal ecology," says Shelford (1915, p. 10) "structural adaptation is usually conceived as of secondary or tertiary importance." The statement has been emphasized by recent ecologic trends. It is doubtful indeed that structural adaptation holds even tertiary place among ecologic concerns of the past decade.

Here paleontology offers a sharp contrast. "La paléontologie éthologique," says Louis Dollo (1909, p. 418), "C'est la paléontologie de l'adaptation." Structural adaptation figures largely in the work of Dacqué (1921), is the keynote of Abel's "paleobiologic" studies (1912, 1921) and figures largely in the works of Lull (1929), Berry (1929), and Hennig (1932). Does not this indicate another significant distinction between paleontologic ecology and that of modern organisms?

Though Dollo uses Geoffroy's term ethology, he does so in a sense too limited to be consistent with the original meaning. His review of the "conditions of existence" (zones, light factors, and modes of life) is bounded by the classical concept of adaptation, and deals only with marine invertebrates and lower vertebrates. Even Hennig, who follows Dollo in terminology, greatly expands the field.

The other authors mentioned use structural adaptation either as a phase of evolution or as data of paleobiology, which is interpreted as the adaptive natural history of fossil animals, not the general biology of the past that its title implies. They do not suggest that such adaptations are a major, or an important part of paleoecology.

This does not mean that study of adaptations should be relegated to theoretical evolution. It is true that paleoecology is concerned with whole organisms, not the specific organs in which adaptations generally are found. Yet if an organ shows striking environmental relationship, that relationship affects the entire body and perhaps many of its neighbors. Thus the boring radulae of *Polynices* and

Urosalpinx may be called structural adaptations, but they determine the food habits of these snails and their place in communities. Similar radulae, in snails of Ordovician to Pleistocene age, are evidenced by abundant bored shells. Here an adaptation, even indirectly determined, possesses autecologic and synecologic significance.

In so far as adaptations are thus employed, there are valuable data of paleoecology. Yet certain cautions must be observed:

1. Adaptations without corroborative stratigraphic or functional evidence may be misleading, especially in motile organisms. Conflicting opinions as to movement of trilobites, the functions of the bulb in *Scyphocrinus*, and the use of the tusks of *Dinotherium* are cases in point. Adaptations may be used to imply environmental conditions only if evidence is very clear, lest reasoning descend to a Lamarckian circle.

2. Many adaptations refer to vertical locus rather than habitat or environment (Shelford, 1915, p. 10). The most conspicuous structural adaptations of terrestrial animals are those involved in digging, running, climbing, or flying. Yet animals with these varied habits and structures occur in all possible situations, with little regard for the climatic or physiographic backgrounds of their layer societies. This is evident if we compare animals of desert, rain forest and savanna: "the primary ecological divisions are to a considerable degree out of relation with the adaptations, as burrowers, runners and climbers occur in all three habitats."

This discordance is less marked in plants than in animals, in marine forms than in terrestrial. Yet always it must be borne in mind, and checked by varied data.

3. In the majority of paleontologic studies, adaptations have been used as evidence for Buffonian, Lamarckian or Darwinian theories of evolution. Such use is legitimate, though often uncritical, as Romanes (1895, pp. 159–287) and later authors have shown; but it is not a part of paleoecology. It is theoretical evolution: a field which ecology may enter as a tool, but which it does not include.

Indeed, it seems that the narrow limits of classical adaptation, which concerns itself with special or conspicuous structures and functions of real or fancied value to their possessors, removes it from profitable consideration in paleoecology. Decades of fact-finding and speculation by biologists have left the problem where it was in Darwin's day. Yet biological materials are more suited to sound results than are the best or most abundant fossils.

As data of succession, function, and survival accumulate, paleoecology may concern itself profitably with the larger concept of fitness as conceived by Whewell (1834) and Henderson (1913). It also may contribute largely to the historical aspects of evolution, though in doing so it will enter another field than its own.

Taxonomy.—Though not part of paleoecology, taxonomy is important to it. Taxonomy provides the means for determining and listing the or-

ganisms composing communities—work that must be done with care if it is not to result in confusion. In the second place, each species or subspecies has a fairly definite ecologic character, and so far as this character is known, it permits ecologic conclusions to be drawn even from faunal lists.

Many species, however, consist of ecologically different forms, such as the isopods studied by Allee (1912), the *Cardium edule* examined by Kindle (1930, p. 12), and many madreporarian corals (Vaughan, 1907). Thus two associations or cenoses containing several species in common might have widely different ecologic make-up. On the other hand, communities widely separated areally, chronologically, and taxonomically may contain species ecologically similar. Rain forests of South America and Africa, sandy bays of the present and the Cambrian, and algal and stromatoporoid biostromes are examples of ecologic similarity despite taxonomic distinction.

METHODS AND PROBLEMS

Autecology of fossils.—Data determining the environmental relationships of fossils and fossil communities will be drawn largely from the field of autecology. They will include:

1. Evidences of environmental factors and relationships provided by enclosing sediments, the positions of fossils in them, and the condition of these fossils as parts of the sediments. These may be grouped as *sedimentary* or *sedimentologic data.*

2. Evidences of function provided chiefly by preserved life positions, and by traces such as burrows, trails and tubes. These may be classed as *functional data.*

3. Evidences of both function and environmental conditioning found in morphologic characters, or inferred from them. These must include all distinguishably significant characters, not merely the striking ones to which "adaptations" may be applied. Their contributions may be grouped as *morphologic data.*

Each of these groups presents its own problems and requirements in method. The first, except in viewpoint, is part of sedimentology, as had been shown by Twenhofel (1931, 1932, pp. 147–183) and Matthew (1932). It requires both examination of strata containing the fossils in question and comparable ones forming at present; it demands a great deal more detail in stratigraphic descriptions and sections than is customary at present. Hadding (1927–1932) has shown how much information of environmental value can be derived from even gross characters of sediments. Belanski (1927–1928) applied more conventional sedimentary data to a detailed study of environmental changes in both area and time. Sandidge (1928) has applied an intermediate method to the ecology of recurrent *Kingena* association-types in the Lower Cretaceous of Texas.

Both sedimentary and functional data are provided by the positions of fossils in rocks. Some lie where they fell or were washed; others stand in

positions of growth. The contrast is well shown by the drifted shells of *Lingula* figured by Hall (1852, pl. 4) and the upright shells of *Lingula*, *Porambonites*, and *Clitambonites* described by Öpik (1930, pp. 39–41).

Wear or corrosion of fossils shows equal variability in meaning. The worn shells of coquina, the fragments in many limestones, and the rounded stromatoporoids of some biostromes show the action of physical factors.[3] So does corrosion of umbones in clams and some brachiopods. But wear of brachiopod umbones, and borings made by annelids, sponges, algae, and even brachiopods provide functional data for both builders of the affected structures and the borers. Here is a field for significant, yet simple investigation, for little is known of the living positions of fossil brachiopods. Studies by Mrs. Fenton and the writer (1932, 1932a, 1935a) show that suitable material is more common than sometimes has been thought.

For vagile animals and some littoral plants, functional data may be derived largely from traces. Here lies the major import of trails, burrows, and the like to the autecology of fossils. Interpreted by comparison with modern traces, they show both the nature of their makers and behavior. Though chiefly produced by animals, algae and higher plants are represented—a case in point being the discovery of an *Egregia*-like kelp in Cretaceo-Eocene sandstones near Carmel, California.

The interpretation of morphologic data rests partly upon direct analysis of structures and partly upon comparison with living forms. The former is specially suited to sessile animals and plants, though it is extensively used in reconstructing the habits of aquatic and terrestrial vertebrates. The latter may take one of two paths. The most frequented is that in which morphology is applied taxonomically, with resulting correlations of habit and environment. Thus we conclude that brachiopods and corals are marine, that palms signify warm climates, that calcareous algae mean shallow water. The method is valid yet possesses limitations. We may not assume that Paleozoic telotremates are ecologically equivalent (within the marine environment) to modern telotremates. Even greater distinction separates some living Demospongiae and their apparent Paleozoic relatives (Twitchell, 1929). Kirk (1928) has thrown doubt upon the marine temperatures inferred from Paleozoic corals, a doubt strengthened by study of brachiopods.

The second method, that of direct comparison, is less uncertain in results. It often cuts across taxonomic lines, as in Dollo's study of the amphipod *Cytosoma* to determine the habits of the trilobite *Aeglina* (1909, pp. 411–414). It also may employ characters only superficially struc-

[3] This seems to ignore the importance of many mud-eating and other organisms in comminuting shells and tests. Since these affect tests as massive as those of sand dollars, they are significant in sedimentation. Unfortunately, it does not seem possible to assign to fragments thus produced definite significance as the products of organic activity. Without it, they do not become biotic factors in paleoecology.

tural, such as cephalopod coloration (Ruedemann, 1921; 1921a; Foerste, 1930.)

Synecology of fossils.—The synecology of fossils is distinguished by its attention to communities. It involves two major procedures: the assembly and synthesis of autecologic data, and the statistical study of fossil communities. The former will provide information on interrelationships and environmental tolerance or resistance. The latter will give at least approximate ideas of numbers, or relative importance of forms, and of communal response to the environment. So far as materials permit, the two provide a sociologic analysis of fossil communities that may be strengthened by comparison with those of the present.

The qualification, "so far as materials permit," is important. No fossil assembly includes all the organisms or all the kinds of organisms composing it during life. Few fossil assemblies of size are free from the remains of organisms that have drifted in after death. Many assemblies lies in neither the communities nor the environments of life, but, as Wasmund (1926) and Twenhofel (1931, pp. 417–419) have shown, consist of organisms which perhaps lived in one place, died in another, and were buried in a third. Still others, such as those of the Cincinnatian Southgate formation, show extensive disturbance after initial burial, with consequent loss of primary stratification and ecologic grouping.

Such cases show the need for the terms "faunule" and "zonule" in paleoecology. First used by Williams (1903) in conflicting senses, the former has been redefined as "an assemblage of fossil animals, associated in one or a few contiguous strata, and dominated by the representatives of one community, commonly either an association [cenosis] or a layer society" (Fenton and Fenton, 1928, p. 14). The botanical equivalent, "florule," may be defined by substituting the word "plants" for "animals."

A faunule or florule thus is a community minus organisms not preserved and plus extraneous, but uncertain additions. Strict adherence to ecologic standards might demand the use of these terms in every case, since all fossil assemblages are considerably modified; but such rigid caution seems unnecessary. Especially if attention is focused upon dominants and subdominants, the use of purely ecologic terms in paleoecology seems justified. One may distinguish bottom and bryozoan-frond layer societies in some Cincinnatian and Richmondian horizons, while the Silurian bioherms of Wisconsin, Illinois and Indiana rank as cenoses or associations in which layer societies sometimes may be distinguished. So do most biostromes, such as the *Cryptozoön* "reefs" of New York, the *Collenia* and *Newlandia* zones in the Belt series of Montana and Arizona, the Devonian stromatoporoid biostromes of Michigan and Iowa, and those formed by *Gryphaea* and *Exogyra* in the Cretaceous of Texas, New Jersey and other regions.

The most reliable results of statistical, or detailed descriptive study,

will come from such compact communities as bioherms and biostromes. Yet formations in which fossils are abundant, show evidence of fairly rapid burial, and are found in deposits of quiet waters are almost equally suitable. Some divisions in the Richmond, the Hamilton of western New York and Ontario, and the Hackberry of Iowa yield to synecologic study. The fact that a census must be made from dead materials accumulated through a period of uncertain length is less discouraging than it may seem. If conditions are uniform through the thickness selected, these remains will give a good idea of relative numbers in the community, as well as of relative size of species and their layer relationships. Any of the formations just mentioned can serve as material for work comparable to that of Pearse on communities of Nahant (1913) or Weese and McNab on mud-bottom sera (1930).

In some cases, graphic restorations aid greatly in visualizing the communities of fossil-bearing strata, and facilitate comparison with modern communities. Few restorations have been made for ecologic purposes, yet even those prepared for museum exhibit or popular illustration have shown themselves useful. Ecologic studies of fossils illustrated by restorations will prove more valuable than those limited to descriptions, tables, and figures of specimens.

Geologic applications.—So much has been said of geology's possible contributions to paleoecology that reciprocal services should be mentioned. They promise to be of three principal types: historical, correlative, and sedimentologic. The historical services have been summarized by Vaughan (1924, p. 331):

"The history of most sedimentary geologic formations is in large measure deduced from premises derived through the study of the ecology of living organisms. The temperature of the seas in which the ancient deposits were laid are (*sic*) inferred almost exclusively from biologic evidence. Depth is inferred both from organisms and the nature of the sediments. The intensity of light is inferred from depth and latitude, which controls the angle of incidence of the sun's rays. The character of the motion of the water is deduced from physical features and arrangements of the sediments and from biologic evidence. The concentration of salts in the water is deduced from the organisms. . . . We need to know for geologic purposes the ecology of all the important groups of marine organisms; and the ecology should not be considered merely in an empirical way but it should be based on the deepest ascertainable mechanical and biochemical foundation."

Vaughan might have added that the deductions which he deems essential are made by paleoecologic studies; his emphasis on marine organisms is in keeping with his topic, oceanography. The last sentence quoted becomes even more true if the word "marine" is deleted.

Correlation is based upon the distribution of organisms through time and space. Though its practical con-

clusions, as exemplified in the stated ranges of index fossils, may be applied without thought of paleoecology, their understanding and use in complex situations demand it. The distribution of varied Pleistocene faunas and floras is an ecologic as well as a stratigraphic problem; some littoral formations can be correlated only by paleoecologic methods; and the same is true of limestone zones in the upper Devonian of Iowa. Correlation of zones with recurrent association-types is similarly dependent on paleoecology.

Its services to sedimentology are seen in the studies of Richter (1922) and Twenhofel (1931, 1932), and in economic fields by those of White (1932), Gruner (1922), and many others. North's book (1930) on limestones of the British Isles emphasizes commercial use of those limestones, yet gives extensive paleoecologic data. Almost any rock or mineral deposit which is derived largely from the bodies or through the activities of organisms is susceptible to paleoecologic interpretation. As a rule, the greater the number of organisms concerned, or the greater their contribution to the total mass, the more definite is the need for such interpretation.

CONCLUSION

As the ecology of the geologic past, paleoecology combines biologic viewpoints and data with paleontologic and geologic materials and methods. The result is a subscience which contributes significant backgrounds to such biologic studies as evolution, biogeography and ecology *sensu stricto*. It organizes on a biologic basis scattered facts of taxonomy, stratigraphic paleontology, stratigraphy, and sedimentology, offering valuable aid to these and to historical geology. Primarily, however, it is concerned with the sociology of fossil organisms, both plant and animal; and any narrower conception will hamper both its development and its usefulness.

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ECOLOGY OF BLACK MUD SHALES OF EASTERN NEW YORK[1]

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ABSTRACT

Views regarding the conditions of deposition of black shale are reviewed. It is agreed that dearth of oxygen and accumulation of organic matter faster than it can be oxidized are the controlling factors. Black shale faunas are either purely planktonic or mixed planktonic and benthonic. Lithologic differences accompany the two sorts of faunas. The characteristics of these two are considered in detail and the conclusion is reached that the deposition of black shales was not restricted to small areas or to short intervals of time, but that it extended over large areas and continued for long time. The locus was at the deeper levels of the littoral or at the bottom of troughs, in either case where currents could bring in the plankton fauna freely.

Ecology is defined as the science of relations of organisms to each other and the surrounding world. I should, therefore, approach the problems of the origin of the black shales principally from the bionomic side. Because I have done so already in several papers, I shall not repeat the details, but I shall give here only a brief survey of my conclusions, together with a short introduction, and then emphasize new physical points that serve to support the earlier views.

For an introduction we can best use the chapters on black shales in the excellent *Treatise on Sedimentation* (pp. 200 and 294) by Twenhofel, who gives the following summary of the characteristics of black shales:

> The shales are thinly laminated, but this is not invariable; they may have extensive linear distribution; thinly laminated sandstones are distributed through them to a greater or less extent; there are occasional bands of conglomerate; the most abundant fossils belong to the plankton; some fossils have here a wide distribution; there is a sparseness of benthonic forms; carbonaceous and bituminous shales are not infrequently interstratified with coal beds. Any explanation relating to the origin of carbonaceous and bituminous shales must harmonize with these characteristics.

Twenhofel then presents the different theories that have been advanced to explain the origin of the black shales, namely those of Clarke (1903) and Schuchert (1915), who believe that typical black shales (Clarke in case of the Genesee shale, Schuchert in that of the Kupferschiefer) were deposited in "closed arms of the sea," with perfect "dead grounds" at the bottom (Schuchert), or by earlier "Black Seas" (Clarke); further that of Ulrich (1911) and Ruedemann (1911), who simultaneously claimed for the black graptolite shales seas with free ingress and egress, as the graptolites were plank-

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tonic animals of the opean ocean and not of epicontinental habitat and had to be brought by oceanic currents into the epicontinental seas. According to the last view these shales were deposited in deeper, quiet levels along the coast lines, for instance, in the Appalachian geosyncline from Newfoundland to Alabama. Ulrich has more fully developed his views in the *Revision* (1911). Finally, Grabau and O'Connell (1917, 1921) have concluded that the black graptolite shales of Scotland, which they studied, were "mud deposits on the flood plain and in the lagoons of a large delta or series of deltas where periodic high tides washed the planktonic graptolites and stranded them on the flats." Grabau (1929) developed this view still more until he arrived at the conclusion that great seismic floods or "tidal waves," such as occur in China, may have carried the graptolite muds far inland and deposited them there as graptolite shale.

We may briefly add a few of the more important papers relating to black muds and their problems that have appeared since Twenhofel's treatise, and then will test the black shales of eastern New York in the light of the criteria obtained.

We may first mention K. Andrée's important paper, although it appeared earlier (1916), *Über Sedimentbildung am Meeresboden*, because it emphasizes the fact that both Barrell and Grabau have given the term "delta" too wide a definition, using the term for terminal river-deposits in *sinking* basins, whereas real deltas do not form any thick deposits, such as the graptolite shales.

Of still greater importance for the understanding of the graptolite shales is a paper by Marr (1925) on the *Stockdale shales of the Lake District*. Marr shows in this paper that the richly fossiliferous black Silurian graptolite shales of Great Britain were deposited in two embayments that extended eastward from the Atlantic, where they were wide open, across Great Britain into Scandinavia and Middle Europe. The water in these embayments below the 100-fathom line, where the black graptolite shales and the associated greenish-gray and red barren shales were deposited, was highly toxic, owing to the quietness of the bottom water, lack of vertical circulation and resulting lack of oxygenation. Great quantities of organic matter (seaweeds and planktonic animals) that had been carried into the embayments by storms and currents were dropped into the dead bottom waters. As plankton and pseudoplankton (including epiplankton) found associated in the shales are cited graptolites, certain crustaceans, and small cephalopods.

Ruedemann (1926) analyzed the faunal facies difference between the black Utica graptolite shale and the succeeding gray Lorraine shales and found that the two are composed as shown in the table opposite.

The analysis shows that while the black Utica shale is characterized by a preponderance of sea-weeds, sponges, graptolites, worms, cephalopods, and eurypterids, and by the

Analysis of the Faunas of Black Utica Shale and Gray Lorraine Shale

	Black Utica shale	Gray Lorraine shale	Percentage of black Utica shale	Percentage of gray Lorraine shale
Plants	5	1	4.6	0.5
Sponges	11	...	10	...
Corals	..	1	...	0.5
Graptolites	23	8	21	3.8
Crinoids	..	4	...	2.0
Worms	9	4	8.3	2.0
Star-fishes	1	...	0.5	...
Bryozoans	4	32	3.7	15.3
Brachiopods	12	33	11.1	15.8
Pelecypods	5	63	4.6	30.1
Gastropods	4	30	3.7	14.4
Cephalopods	13	6	12	2.4
Trilobites	7	11	7.4	5.3
Ostracodes	4	13	37	6.2
Cirripedes	1	2	0.5	1.0
Phyllocarids	2	...	1.0	...
Merostomes	6	1	5.5	0.5
Total	108	209		

absence of corals and crinoids; the gray Lorraine shale shows a large percentage of bryozoans, brachiopods, pelecypods, and gastropods.

The smaller fauna of the Utica shale consists of plankton (most graptolites and some cephalopods) and an impoverished bottom fauna, mostly of small forms, and of brachiopods with phosphatic shells; that of the Lorraine by comparison is composed of a normal muddy-bottom fauna with many bryozoans, pelecypods and gastropods.

In the same paper the writer also emphasized the difference, already indicated in the monograph of the New York graptolites (1904, 1908), between the "pure graptolite shales" which contain nothing but graptolites and the "mixed graptolite shales," which also contain a usually scanty and impoverished bottom fauna. We will discuss this point in a later chapter.

A paper that has an important bearing on the apparent absence of faunas in black shales was published recently by Richter (1931) in regard to the Devonian Hunsrückschiefer, famous for its beautifully preserved pyritized star-fishes and crinoids. It has been generally inferred that the Hunsrückschiefer accumulated in toxic bottom water and that the fossils found in it were dropped into this quiet deeper water. Richter, however, shows by the presence of small ripples, cross-bedding, sandstone lenses, and the drifted positions of the crinoid and star-fish arms that the water was in motion; and, further, by the presence of numerous branching worm-burrows (described under the name of *Chondrites* as sea-weeds) and the occurrence in some places of impressions of pelecypods, gastropods, trilobites, etc., that there was a rich benthonic fauna. The absence of the tests of the latter is explained by "selective diagenesis" of the hard parts, by which many were dissolved before the mud was hardened and only those preserved that readily became pyritized. Richter's work serves as a timely warning against too ready an assumption that apparently barren black shales were derived from dead black muds. His extremely suggestive studies in the "Wattenmeer" of the North Sea have shown that dead black mud, loaded with H_2S, is rapidly covered in the sea, through the oxidizing action of the circulating water, with a

white oxidized film, upon which a rich bottom fauna can live. It is obvious that many problems of black shale deposition await solution by study of present processes of deposition.

In a paper on *Paleozoic plankton of North America* (Geol. Soc. Am., Mem. 2, 1934), the writer has brought together the fossils that as rare occurrences have been found associated with the graptolites in the pure graptolite shales. There he reached the conclusion that in character, composition, relative size, etc., they closely correspond to the present fauna of the sargassum-weeds in the Sargasso Sea; and that the graptolites as a whole belonged to the pseudoplankton. They drifted far and wide attached to the Paleozoic seaweeds that formed sargasso-meadows in the central parts of the Atlantic and Pacific Oceans. They were carried into the embayments and epicontinental seas, and there were deposited with the black muds.

A number of recent publications, mainly by zoologists, give information on black mud occurrences and their faunas and serve above all to emphasize the fact that black mud may form at various depths and at various places, as pointed out by Twenhofel (Ibid. p. 203). Yonge (1930, p. 125) found it even at the Great Barrier Reef of Australia, thereby showing that barren black mud formation is not restricted to cold or cool climates, as often claimed. He writes:

> Dredging in the region immediately around Low Isles was undeniably dull; the bottom consisted of a thick, very fine grained, black mud which quickly filled the dredge, but which after being put through the sieves, was found to contain hardly a living beast

As a rule, the black shales are found today at the bottom of more or less enclosed seas, as the Black and Baltic Seas, in bays and fjords with weak tidal action, and along coasts between or behind islands.

It appears from all investigations of black mud formations and faunas that the controlling factor is the relative lack of oxygen and the accumulation of organic matter faster than it can be oxidized. The black color, according to Petersen and Jensen (1911), is due mainly to ferrous sulphide, resulting from the reduction of sulphates by anaerobic bacteria; the original organic material is brown in color. The toxic quality of the bottom water is mainly due to the presence of H_2S and the lack of free oxygen.

After this brief statement of the ecologic criteria of black mud formation, we can more readily analyze the ecologic factors of the Paleozoic black shales of New York.

The Paleozoic black shales are the following:

The Paleozoic black shales are the following:

1.	Lower Cambrian	Black shales
2.	Lower Canadian	Schaghticoke shale
3.	Middle or Upper Canadian	Deep Kill shale
4.	Lower Ordovician	Normanskill shale
5.	Middle Ordovician	Snake Hill shale
6.	Middle Ordovician	Canajoharie shale
7.	Middle Ordovician	Schenectady shale
8.	Middle Ordovician	Utica shale
9.	Lower Silurian	Shawangunk grit and black shale
10.	Middle Devonian	Marcellus shale

TWO GROUPS OF BLACK SHALE FAUNAS

We have already seen that these black shales can be divided into two distinct groups, those that had a purely planktonic fauna and those that had a mixed, partly planktonic and partly bottom fauna. To the first group belong undoubtedly the Schaghticoke, Deep Kill, and Normanskill shales, and probably the black Cambrian shales; to the second the Snake Hill, Canajoharie, Schenectady, Utica, and Marcellus shales. All of the latter have a prevailing planktonic fauna, (graptolites etc.), but also a more or less impoverished bottom fauna. The Shawangunk grit and black shale is in a place by itself and will be mentioned later.

The first group, especially the Schaghticoke, Deep Kill, and Normanskill shales, contain planktonic faunas, if any. The fossils of the Lower Cambrian black shales are unique specimens, so rare that they are obviously accidental invaders of the sedimentation area and of no critical value. The faunas of the three units noted first have been fully discussed in another paper and have been shown to be completely planktonic, derived from a Sargasso Sea. They consist of the multitudes of graptolites, small sponges, rare fleshy cnidarians, minute brachiopods with phosphatic shells, annelids, very few small molluscs, and crustaceans of peculiar type (*Caryocaris*, *Discinocaris*, *Eunoa*). A flora of seaweeds is also present. All these are of types similar to those now living on *Sargassum*, the graptolites taking the place of the present bryozoans.

PHYSICAL CONDITIONS OF BLACK SHALES

The evidence from the faunas is fully supported by that of the physical conditions of the beds. The following facts are noted in this connection.

1. There are no casts of fossils in the pure graptolite shale, indicating the former presence and later destruction of fossils; nor are there any trails that would indicate organic bottom-life, such as Richter records from the Hunsrückschiefer. There are, however, trails in certain layers of the green and red slates associated with the Cambrian black shales, as in the slate with *Dactyloidites bulbosus*. Trails and worm-burrows, on the other hand, are in evidence in the mixed graptolite-shales, as the Utica and Snake Hill, strengthening the evidence of bottom life furnished by the shells.

2. It is in line with this evidence that the pure graptolite beds not only contain fully grown colonies, but that they are crowded with growth stages of all sizes and species. The presence of many young forms in a black shale indicates, as pointed out by Richter, catastrophic destruction. Richter uses the absence of young forms in the Hunsrückschiefer as good evidence of the undisturbed growth of the faunas there. Vice versa the abundance of growth stages in the graptolite shales indicates the settlement and burial on

the bottom of the entire graptolite life of that region after a storm that destroyed and tore up the carrying sargassum-floats and tore to pieces the free-floating colonies.

3. On the other hand, while the entire graptolite fauna settled to the bottom much broken, it was preserved without destruction of the thecae by bottom scavengers. In most beds the graptolites are beautifully shown, though compressed, and also the few other planktonic forms are in perfect condition; the writer for instance, figures in the paper on Paleozoic plankton a splendidly preserved, small actinian (*Palaeactinia halli*) from black graptolite shale.

4. The absence of oxygenating currents in the places where the graptolite shale was deposited is proved by the almost entire absence of any parallel arrangement of the graptolites in the pure graptolite-shales. On the other hand parallel arrangement is often seen in the mixed graptolite shales, as notably the Utica and Canajoharie shales. The writer once (1897) inferred the presence of a northeast-southwest current south of the Adirondack uplift from the parallel arrangement of graptolites and small cephalopods in the Utica and Canajoharie shales of the Mohawk Valley, an observation that is well supported by later paleogeographic studies. The movement of the water was, however, in every case weak, not strong enough to carry the graptolite fragments away.

5. It is in line with the evidence from the lack of parallel arrangement that many of the pure graptolite shales contain pyrite nodules. In some beds of the Deep Kill shale graptolites, especially specimens of *Phyllograptus*, frequently form the centers of pyritized nodules. As the graptolites in the concretions are fully preserved without any distortion whatever, while the others are compressed into flat films, it is obvious that the pyrite concretions must be of syngenetic origin. If they formed at the time of the deposition of the shale, there can be no doubt that the bottom mud and water were strongly charged with H_2S. Pyrite is also found in the mixed graptolite shales, but in less obtrusive quantities. Graptolite rhabdosomes in the Normanskill shale are found filled with pyrite and thereby preserved in relief.

6. The pure black graptolite shale is usually thin bedded, and the graptolites are found spread out on the bedding planes, more rarely or not at all within the shale. As the bedding is evidence not so much of the fixation of movement of material as of its cessation, the graptolite-covered bedding planes indicate periods of great quietude at the bottom, already suggested by the lack of parallelism.

7. The pure black graptolite shale, as also the black Cambrian slate, is always found associated with red, green and greenish-gray shale and slate. This association is entirely absent in the mixed graptolite shales, such as the Canajoharie, Utica, Snake Hill and Schenectady shales. The red, green and greenish-gray shales are the result of deposition in

foul or "poisoned" water, as Marr has clearly shown in the case of the Stockdale shales. These shales, both in the Cambrian and Ordovician of eastern New York, are utterly barren of fossils; the *Oldhamia* and *Dactyloidites* of the Lower Cambrian slate, the first from the red, the latter from the green slate, are exceptions that confirm the rule, especially as both are still Problematica, possibly sea-weeds.

The red and green muds have nothing to do with the red and green ooze of the abysmal depths, but are clastic sediments brought down by rivers. As the conditions at the mouth of the Amazon (see Twenhofel, p. 548) indicate, red muds that were red when first deposited may become black or grey under the red surface. Organic matter decaying under the anaerobic conditions changes the hydrous ferric oxide into sulphides or carbonates. The red shales therefore not only indicate a warm, mostly tropic, moist climate of the country at the time, but also a temporary lack of organic material in the deposits.

8. The Deep Kill, Normanskill, Snake Hill, and Schenectady beds contain intercalated grit and sandstone beds, often of considerable thickness, especially in the middle Deep Kill and the Normanskill shales. These beds are entirely barren, save for a few graptolites scattered on the bedding planes, but even a thin black film intercalated in the grit (Middle Deep Kill, Ash Hill beds) may contain numerous graptolites. Also thin conglomerate bands may occur. These grits, sandstones and conglomerate bands have been cited frequently as evidence of the shallow-water, near-shore deposition of the graptolite beds. Shepard (1932) has, however, shown that the old generalization of a simple gradation of coarse into fine sediment across the continental shelves is as rare as is the occurrence of graded topographic profiles. The typical arrangement of a sediment on the open shelves is patchy, with almost haphazard mixtures of mud, sand, and gravel all the way to the outer margin. Shepard found that muddy sediments on the outer shelf are rather unusual, even off large rivers, and that the finest sediments are found in bays near shore. This of course does not include the lower slope, free from wave-action, nor do we have in the Appalachian geosyncline and adjoining epicontinental seas the conditions of a continental shelf, fully exposed to the onslaught of an open ocean. It is quite possible that the distribution of the grits and black and gray shales of these formations is patchy, and that the graptolite shales change horizontally into other sediments. The absence of ripple-marks,[2] sun-cracks and even of cross-bedding in the Deep Kill and Normanskill beds is sufficient proof, in spite of the presence of the sand and grit beds, that those beds were not deposited close to shore or in very shallow water. It is different in the Schenectady beds, where the continuous

[2] I know of only one observation of ripple-marks, viz., in the Normanshill shale, at the Broom street quarry at Catskill.

vertical alternation of sandstone and shale beds, the presence of cross-bedding, and the rapid changes from shale to sandstone horizontally and vertically point to shallow-water deposition and active currents. At the same time graptolite-bearing black shales are decidedly rare in this formation. In the Schaghticoke and Deep Kill shales thin barren limestone bands, an inch or two thick, alternate with black graptolite bands, and green, more or less silicious shale bands through great thicknesses of rock. These regular alternations, almost suggestive of varves, lack all indications of shallow water origin, as well as of current action at the bottom. They may be the result of several combined factors, as change of direction of the currents at a higher level, or slight changes of elevation of the bottom, for, as Walther found in the Bay of Naples, a slight difference of elevation produces there the impoverished fauna of the deeper mud-bottom and the richer fauna of the slightly higher "pigeon-bank"; and finally, according to Andrée (1923, p. 262), the widely different contents of rivers (as of the Nile today) may greatly affect the marine deposits. These different river contents depend on seasons and, on a larger scale, on climatic changes.

The Canajoharie and Utica shales are thick masses (Utica 700 ft., Canajoharie 1100 ft.) of uniform mud-shale and rare impure limestone bands. They were deposited in sinking basins sufficiently far away from the shore not to receive coarser sediments (the upper Schenectady beds with their heavy sandstones may well represent the near shore deposits of the Utica shale). The Canajoharie shale grades westward into the Trenton limestone, and passes by alternating shale and limestone beds (Dolgeville beds) into the upper Trenton, whereas it continues northward through the Champlain basin as black shale. The Utica shale passes northwestward into the Cobourg limestone of Upper Trenton age. In these cases it is obvious that the shale material came from east and northeast, perhaps from rivers, and was spread westward, as is also indicated by the parallel arrangement of the graptolites and other fossils.

9. The pure black graptolite shales differ from the uniform mud beds of the mixed black graptolite shales by the presence of grit beds, thin limestone bands, and thick red, green and greenish-gray shale masses. They are often of restricted extent, as especially in the Normanskill shale, which suggests the possibility of patchy or local deposition in depressions. On the other hand it is important not to overlook the extension of the Schaghticoke, Deep Kill and Normanskill shales practically through the whole Appalachian geosyncline from Newfoundland to Alabama. It is impossible to see in this enormous north-south extension of typical Atlantic graptolite faunas of undoubted oceanic origin anything but the effect of ocean currents sweeping through a wide embayment or intracontinental channel, the

Levis trough. It is further important to remember that graptolite shales occur nowhere in the parallel Chazy trough, where they are replaced by limestones and sandstones, except the Canajoharie shale of Trenton age, which was deposited in that basin. The two basins appear to have been alternately drained and submerged (Ruedemann, 1929).

Even if one should be inclined to accept the view of some that the graptolites were deposited in small quiet embayments, shore lagoons, etc., and even if one should cite the possibly patchy distribution (not yet proven, however) of the graptolites as favoring this view, one still has to assume continuous lagoons and embayments along coasts stretching the full length of the continent—an assumption that would be as exaggerated as Grabau and O'Connell's chart of a series of continuous adjoining deltas to explain the great series of Scotch graptolite beds.

In contrast to the enormous north-south distribution of the Levis trough graptolite beds, the Utica shale shows a wide east-west distribution from the Mohawk valley to the Ohio basin, where it is still present at Cincinnati and in Kentucky. This distribution is readily attributed to the east-west current mentioned above.

10. Not only the wide distribution of the pure graptolite shales is strongly in conflict with their supposed deposition in local embayments, as claimed for them by Twenhofel (1915, 1931), or on deltas, as asserted by O'Connell and Grabau, but still more so the facts that pure graptolite formations, such as the Deep Kill shale are not only of great thickness, in spite of the obviously slow deposition of the fine mud, but also contain a great series of faunas. The Deep Kill shale, for example, contains at least 9 faunal zones (see Ruedemann, 1919, p. 121), which must have taken a long time to evolve and which, therefore, correspond to thick formations of clastic beds (the Canadian and lower Chazyan). Dr. E. O. Ulrich has rightly for many years been outspoken in claiming very slow deposition and long time intervals for the successive graptolite zones. Such a succession of zones as is found in the Deep Kill, over an area extending from the lower St. Lawrence through the Appalachian geosyncline at least as far as Virginia, is, of course, not the result of deposition in little, scattered embayments along the coast. It requires a far-flung sea and a coast line persisting through long intervals of time. Zones are recognized also in the Normanskill shale, but the lack of an undisturbed section has thus far not allowed their elaboration.

11. The mixed graptolite shales, notably the Canajoharie and Utica shales, are likewise divisible into zones (see Ruedemann, 1919, p. 126), the Canajoharie into five zones and the Utica into three. These zones are however not so greatly different in fossil content as those of the Deep Kill shale, but rather are distinguished by the temporary predominance of certain forms in an otherwise fairly homogeneous fauna. It is

therefore probable that these shales, in spite of their great thickness (1100 feet for Canajoharie shale), represent rather rapid deposition in sinking basins with plentiful supply of fine detritus. This is undoubtedly true of the 2000 feet of Schenectady beds, composed of alternating shale and sandstone.

12. The Devonian Marcellus black shale, the lowest Hamilton beds, is found in the eastern or Appalachian section, where it shows a northeast-southwest distribution, grading both westward and upward into normal Hamilton beds composed of gray shales and sandstones. This black fissile shale, about 170 feet thick in the Helderbergs, near Albany, New York, has there no intercalations of other rocks except large limestone concretions at several horizons, and a small amount of intercalated sandy beds at the bottom and the top. At the bottom the sandy layers contain small specimens of *Liorhynchus limitaris* (Vanuxem) and *L. mysia* Hall. At the top the Hamilton species of *Spirifer*, particularly *S. granulosus*, appear. It is apparent that the Marcellus black shale is of the type of deposition of the mixed graptolite shales *minus* the graptolites, mainly because they had become extinct. However, the lack of a planktonic fauna, save the common *Styliolina fissurella*, suggests that this Marcellus epicontinental sea had no such wide-open connection with the ocean as had the Ordovician graptolite-shale forming seas. On the other hand, the wide distribution of the black Marcellus shale from western New York eastward and southward, and its great thickness, leaves no doubt that it was deposited over very extensive fouled bottoms which the circulation of the higher sea levels could not reach.

13. There is still a biotic element in the black graptolite shales that deserves special notice, namely the eurypterids. The writer discovered eurypterid faunas in the Normanskill shale at Catskill and in the Schenectady beds at Schenectady. With the exception of a single species known before from the Utica shale (*Echinognathus clevelandi* Walcott) these were the first Ordovician eurypterid faunas that became known on this continent. The bearing of the occurrence of these rather extensive eurypterid faunas in the otherwise barren or nearly barren graptolite shales has not yet been discussed and was omitted in the writer's paper on planktonic faunas. The recent discovery of other eurypterids, not only in the Normanskill shale, but also in the Deep Kill, Utica, and Snake Hill shales, makes the eurypterids an important element of the graptolite faunal assemblage, and therefore calls for closer investigation of the ecological factors. This problem will be dealt with by the writer in another paper, but it may suffice to state that evidence at hand indicates the eurypterids to be an element entirely foreign to the graptolite beds. The writer does not believe that they possessed a planktonic habitat comparable to that of the peculiarly adapted fishes found today in the floating *Sargassum*-patches; nor is it

necessary to relegate them to the rivers of Ordovician or Silurian time, as many authors do—on fallacious evidence. The writer has already shown the undoubted marine habitat of the eurypterids of the Bertie waterlime, proclaimed by some as river animals. Likewise the eurypterids of the Shawangunk grit at Otisville, N.Y., also considered by various authors as river animals deposited on a delta, contain many very early growth stages, down to 1 mm in size (some of these have been described by Clarke and Ruedemann in *The Eurypterida of New York*), and it is obvious that the creatures lived and were breeding where they died. To the writer it is entirely probable, even if it is assumed that the great mass of alternating grit and thin black shale of the Shawangunk formation was deposited in a sinking delta, that the eurypterids came out of the sea, exactly as their relative *Limulus* does today, to lay their eggs in the shore-sands—in the case of the Shawangunk, in the sands of the lower, marine end of the delta foreset or even bottomset beds. There are no fossils, except the numerous eurypterids, in the shale found in the grit that could throw light on the ecology of the Shawangunk life. A few eurypterids and fish remains have been obtained in the grit, a few seaweeds and a single linguloid (now in the New York State Museum) in the black shale.

Considering that the graptolite shales have been proclaimed delta-deposits by Grabau and O'Connell, and the Shawangunk grit also delta-deposits by Grabau and many other writers, one naturally asks why the graptolites, normally so common in black Silurian shales, are lacking in these black delta-deposits, possibly marine foreset beds, if not the deeper bottomset beds. It is a peculiar coincidence that I discovered the Otisville eurypterid fauna in 1906 while looking for graptolites in the thin intercalated black shale bands of the Shawangunk grit.

The common text-book view that both the fishes and eurypterids originated in fresh water has been recently declared to be entirely fallacious by Walter Gross (1933), after a most critical survey of the early paleozoic Agnatha and fishes. He finds the much discussed "ancestral" fish fauna of the Old Red sandstone to be a worldwide, monotonous fauna, contrasting with the much more varied contemporaneous marine fauna and showing the latter to be the evolving and original fauna. The fresh-water fish faunas of today are but the result of repeated migrations into the rivers and lakes. The growing belief among geologists, especially in Europe, in a more or less freshwater condition of the primeval oceans aids acceptance of the postulate of easy migration of the eurypterids and fishes from less saline oceans than we have today into rivers and lakes and back into the ocean. The center of evolution would then be the oceanic littoral region instead of the freshwater rivers and lakes, for they are too short-lived and too irregular in their physical conditions to permit the production

of new forms of more than specific or varietal rank.

CONCLUSION

In conclusion, the Paleozoic black shales indicate by their contained faunas and lithologic associations the prevalence of somewhat abnormal, toxic bottom conditions that either impoverished or completely prevented all bottom life. It is further evident in practically all our cases of Paleozoic black mud shales that the deposition was not restricted to small areas or regions, or so restricted in thickness that it could have taken place in small embayments and lagoons, or on deltas, as is claimed by some, but requires for explanation the existence of the conditions productive of black mud over vast areas and throughout long intervals of time. Such requirements could be fulfilled, in our view, only at the deeper levels of the littoral regions, as Lapworth concluded some 60 years ago, or at the bottom of the troughs (Levis and Chazy troughs) of the Appalachian geosyncline. Some authors deny the necessity of assuming the presence of separate troughs and barriers in the Appalachian geosyncline. It may interest them to learn that a multitude of close-set borings in the Ruhr district of Germany (Bärtling, 1928) has clearly shown that the Variscan geosyncline began with secondary synclines and anticlines, and that the principal sedimentation took place in the sinking synclines and less on the anticlines. A similar condition prevailed from the beginning in the Appalachian geosyncline and readily explains the complexities of deposition unraveled by Ulrich, Schuchert, Keith, Prindle, Knopf, the writer and others in the northern Appalachian area of sedimentation.

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MARINE BIOLOGY AND PALEOECOLOGY[1]

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ABSTRACT

The boreal fauna of the western North Atlantic offers an opportunity to consider biologic factors affecting marine organisms that may have been important in the past. Boreal faunas have certain characteristics which may be useful in seeking to identify them as fossils. The coastal region alone is of moment, for its fauna is large and fossil faunas suggest relatively shallow depths. Plankton organisms, dominantly copepods, are very important today and must have been important in the past, though seldom found fossil. Pelagic larvae often travel long distances in favorable currents. Some areas are unfavorable to development of larval forms, apparently because of turbulence which prevents normal temperature stratification. Temperature is a very effective factor and change in it may have large influence on life. Pelagic organisms may drift far from their normal habitats today and must have done the same in the past. Benthonic forms are therefore the more reliable in tracing faunal regions.

The object of the present paper is to offer a brief discussion of certain physical and biological factors involved in the production and distribution of ocean populations, which, it is hoped, may prove of interest to paleontologists. An attempt will be made to consider the subject from a paleoecological point of view, and only those aspects which appear to be of a rather basic nature will be mentioned.

PHYSICAL FACTORS

It may be well to begin with a consideration of certain physical conditions which, if not extending back to the Cambrian Period, can be assumed to have existed for at least a relatively long period of time. In regard to hydrographical features, the present ocean basins are generally considered to be, even geologically speaking, very ancient. Again, with the axis of the earth unchanged there must have been over these basins a zoning of temperature away from the equator and a resulting basic system of superficial circulation about their margins not essentially different from that of the present time.

Beyond this margin in the North Atlantic there is at the present time a southerly counter drift along the American coast which roughly follows the coastline. Along the course of this drift minor circulatory systems have been formed, but the general set is southerly, and probably has remained so for a long time.

The extent to which this inner cool drift from the north and the outer warm drift from the south would influence the fauna of any particular locality would depend largely on the

[1] This paper was contributed to a symposium on paleoecology held at the meeting of the Paleontological Society in December, 1933.

configuration of the coastline, and, of course, general climatic conditions. At the present time Cape Cod and Cape Hatteras form the most important demarkations of faunal zones along the Atlantic coast.

In view of the fact that a large proportion of marine vertebrates and with relatively few exceptions, all marine invertebrates have pelagic young, it is evident that in problems involving distribution, and particularly faunal barriers, a consideration of the major current systems is as essential to the paleoecologist as to the marine biologist.

OPEN OCEAN POPULATION

Seaward of the continental slope and within the circuit of the open ocean drift the pelagic surface population of the North Atlantic consists of warm water forms, and the bottom population of species related to the coastal fauna but specialized for an abyssal existence. Although the descent of animals to ocean depths appears to be rather recent in the geological time scale, some of the forms have undergone considerable evolution, as exemplified by the extreme modification of holothurians of the group Elasipoda and the subsequent rise of an abyssal pelagic medusa-like form, *Pelagothuria*, from this group. Considerable radial evolution, subsequent to penetrating ocean depths, is indicated by whole groups of widely distributed forms with common structural characteristics which differ markedly from their coastal relatives. The *Macrurus* and *Ceratias* types of fishes and the above mentioned Elasipoda group of holothurians are striking examples.

Compared with the coastal region, life in the deep sea is relatively very scanty, and consists entirely of consumers (plants are largely restricted to the photic zone). The benthonic fauna in a general way reflects quantitatively that of the upper levels. The greater part of the so-called deep-sea fauna is really found on the lower portion of slopes and ocean ridges in depths of from 1000 to 2000 meters, which has been designated as the archibenthal zone. Life over the abyssal plain is, even in comparison with the archibenthal zone, extremely sparse. Deep water animals are rarely very large, probably because of the mechanical difficulties involved in withstanding great pressure and the lack of sufficient food.

There is little indication that a deep sea fauna is anywhere represented in geological deposits now above sea level. Marine fossil remains described to date appear to consist largely of neritic forms and, to a somewhat less extent, of associations suggestive of the continental plateau or perhaps offshore areas of inland seas. Except for sporadic or temporary seasonal invasions of pelagic open-ocean species, the problems of the marine paleontologist would appear to be largely concerned with populations ranging from the strand line to the slope, with depths rarely exceeding a few hundred meters.

COASTAL POPULATIONS

Supplementing other evidence, the large concentrations of invertebrate

fossils so frequently found would hardly have originated very far from the coastline, except on offshore banks or in the course of some active current system like that along the margin of the continental slope. Since shallow banks usually form vortices for local rotary drifts, pelagic larvae tend to be retained over them until ready to descend to the bottom. In this manner there is maintained a resident benthonic fauna comparable with that of a similar depth zone on the coast. Bottom feeding fishes at the present time also concentrate in these areas, with the result that over large intervening expanses of the continental plateau benthonic life is comparatively sparse. Yet over 90% of the world's fish supply is obtained from the narrow shelf fringing the continents, and it is probable that the relative percentage of the total benthonic invertebrate population found between the tide line and the base of the slope is even larger.

As it is obviously impossible to include all faunal zones of the continental plateaus, even those of the Atlantic coast, in so brief a paper, I shall limit myself to the biology of the so-called "cold water" or boreal fauna.

BOREAL REGION

Although major ocean currents tend to form regional barriers, local concentrations of coastal populations are more intimately associated with minor non-tidal circulation systems of the type found in the Gulf of Maine. These are so readily altered by changes in the character of the coastline that present day conditions must be assumed to be of relatively recent origin. Warmer water north of Cape Cod in moderately recent time is indicated by the presence of isolated relic temperate species in enclosed areas like the Gulf of St. Lawrence, where continued high summer temperatures permit such species as the common oyster (*Ostrea virginica*), now absent elsewhere north of Cape Cod, to survive. Another species, *Venus mercenaria*, is found in Casco Bay. Elsewhere in both the eastern and western Atlantic quantities of sub-fossil shells of present south boreal and temperate molluscs have been reported far beyond their present range. In Europe such finds have been made in northern Denmark and on the Norwegian coast as far north as Bergen. It would appear, therefore, that for coastal conditions the principles involved, rather than the actual distribution of present faunas, will be most applicable to the problems of the paleontologist.

It is probable that boreal-arctic animals will be found to have existed somewhere in the world at all times since the Cambrian Period, and a more intensive study of present "cold water" communities than has as yet been made may reveal indications by which the paleontologist can detect similar conditions in the past. In problems of this sort it seems desirable to consider the general composition of the population rather than the characteristics of individual species or groups, as it is diffi-

cult to select any single morphological character which will definitely distinguish cold and warm water species. Of present boreal-arctic characteristics may be mentioned: (1) Large numbers of relatively few species, contrasted with many species, usually no one particularly dominant, in tropical waters. (2) Definite annual reproductive periods of limited extent (spring and summer), resulting more commonly in detectable age groups. (3) Heavy annuli or growth rings, particularly on fishes and certain invertebrates, denoting a winter retardation of growth although in the case of fish, at least, this cannot be applied to all species. However, if a substantial number of species in a fossil community exhibited such markings it would suggest that they had been subjected to wide seasonal variation in temperature. (4) Absence of hard corals and other reef builders—there is but one common and very small species at the present latitude of New England (*Astrangia danae*). (5) Apparent absence of calcium carbonate sediments of recent origin.

In the western Atlantic the boreal population is centered north of Cape Cod although certain species occur considerably south of this point. The pelagic species, particularly during the cold months, are often found as far south as Cape Hatteras, in some cases even farther. Northward beyond Cape Sable the population becomes increasingly arctic in nature. The slope forms the outer boundary, depth restricting benthonic adults and the circulatory drift (Gulf Stream in the Northwestern Atlantic) together with a resulting temperature gradient affording effective barriers to a seaward movement of most pelagic larvae and adults.

ROLE OF PLANKTON

As elsewhere the distribution of the animal population of boreal waters is intimately associated directly or indirectly with its food supply, plankton, and it is evident from the wide variety of modern planktonic species, as well as the character of pelagic young in almost all marine invertebrates, that it has played an equally important role throughout the course of evolution in ocean life. Unfortunately, because of their small size plankton organisms are rarely found in fossil deposits. However, one can safely conclude that large quantities of fossil bottom invertebrates so frequently found, were distributed in a very definite manner with respect to tidal and non-tidal currents, being transported in larval stages as planktonts to their final locations and through the same agency maintaining themselves with a continuous supply of plankton food. A consideration of the biology of zooplankton may then be expected to prove of practical value to the paleoecologist concerned with the distribution of larger invertebrates and fishes.

COMPOSITION OF ZOOPLANKTON POPULATIONS

Offshore over the greater part of the boreal region the zooplankton throughout the year consists of

a true pelagic association, supplemented during breeding seasons by larval fishes and in relatively small numbers by bottom invertebrate larvae. A few benthonic adults, particularly among the annelids and crustaceans, become free swimming for short periods during the breeding season and at such times often swarm at the surface. Near the shore the summer pelagic population may be dominated by benthonic invertebrate larvae and neritic plankton species. With the decline in temperature in the autumn the latter pass into a resting stage and the winter population, derived from offshore, becomes relatively uniform over the entire region.

Although most groups have pelagic representatives, Crustacea comprise the greater part of all zooplankton except during the summer breeding period, when local swarms of other larvae sometimes dominate in restricted areas for brief intervals. Over the Gulf of Maine, even during the period of most active breeding, from April to September, Crustacea in 1932 averaged 91 per cent by number of the total zooplankton population, and in September ranged as high as 97.6 per cent.

IMPORTANCE OF COPEPODS

Copepods are by far the most numerous multicelled animals in the sea. In the Gulf of Maine one species, *Calanus finmarchicus*, averaged 42.9 per cent of the total zooplankton population from April until September. As many as 3700 individuals per cubic meter have been reported, and at times the numbers probably exceed this. When it is considered that the benthonic population is limited to a thin film over the bottom while this form is distributed through a column several hundred meters deep, these figures assume even greater significance. Under one square meter of surface 33,700 individuals of *Calanus* have been taken. The total benthonic population is relatively small compared with this single species, but in the natural economy of the region the difference in size must be considered. The copepod content of the summer zooplankton stock in the Gulf of Maine averaged 75.4 per cent in 1932.

AUGMENTATION OF ZOOPLANKTON

Propagation in the boreal region begins in the spring and terminates in autumn. Being closely correlated with temperature, in each species the particular time of spawning is largely governed by the locality. Most arctic species spawn in mid-summer in arctic waters, but those ranging into the boreal region spawn much earlier in the season. In a similar manner boreal species establishing themselves south of Cape Cod tend to spawn as early as late winter. However, within the normal confines of their range most boreal adults begin to spawn first in March and April in the southern portion of their region, and the response is progressively later northward. Most local species have begun spawning by May, although in a few the peak is in mid-summer, and one copepod (*Centropages typicus*) spawns principally in early autumn.

The boreal stock is at a minimum in late February and early March. In the zooplankton, indicative of production of both pelagic and benthonic species, there is a slight rise from March to April followed by an enormous increase from April to May. In 1932 the volume of zooplankton rose 348 per cent during this time. There follows a very rapid decline from May to June (38 per cent in 1932) and a more gradual decline throughout the remainder of the year in spite of the addition of subsequent crops. It would thus appear that either far more animals are produced during vernal augmentation than the area can support and the heavy mortality takes place as the balance is restored, or the interval of maturation, falling at this time, forms a critical period during which a large part of the dominant copepod stock dies out. Recent findings support the latter suggestion.

In most of the boreal benthonic and larger planktonic species there is just one generation each year. Growth is rapid during the summer but proceeds very slowly after the decline in temperature in the autumn. With the warming of the water in the following spring these forms mature rapidly and spawn. In the greater part of the invertebrates personally observed, maturity is reached in a maximum of one year, and yearlings form the major portion of the parent stock, indicating that the population is largely replaced each year. In some of the larger species like the lobster a longer period is required. The dominant species of offshore copepods, which form the most important source of crustacean food, have at least two well defined breeding seasons and possibly a third during the summer. These represent successive generations.

DISPERSAL

The quantitative distribution of adult zooplankton and bottom invertebrate populations serves as a measure of the result of production on different areas, but does not in itself necessarily indicate the point of origin. Neither does it serve as a positive measure of the productivity of various areas. It is probable that the young of few benthonic invertebrates reach the bottom very near their starting point. With dominant nontidal sets characteristic of coastal waters, the existence of most bottom communities is dependent either on an enclosed circulation system or, in the case of an along-shore drift, on other aggregations so situated in the direction of the set that they serve as sources of supply.

The distance traveled by pelagic larvae is often surprising. Along the coast of Maine during the spring period of most active propagation, coastal drift velocities from eastern Maine to Massachusetts Bay have been found to range from 5 to 8 miles per day. Velocities of this magnitude would permit pelagic eggs and larvae of even temporary members of the plankton, such as the cod, to travel from eastern Maine to beyond Cape Cod before seeking the bottom, a condition which has led ichthyologists to conclude that the region east

of Cape Elizabeth to the Bay of Fundy constitutes one of the most important sources of cod fry found in bottom stages on the rich fishing banks off southern Massachusetts. Eggs produced at any point in the Gulf of Maine may be distributed throughout the region. With a minimum pelagic period of at least 30 days the average invertebrate larva would be expected to travel at least 100 miles before settling to the bottom, unless pocketed in inland waters or a local eddy.

When the drift follows a circuitous route a considerable percentage of the larvae reaching a benthonic stage while over deep water would be expected to be destroyed. As a matter of fact there appear to be other as yet undetected limiting factors which quickly destroy neritic larvae transported offshore. Drift bottles and young of offshore species of zooplankton animals and fishes can be traced around the circuit of the Gulf, but the young of neritic species are rarely found more than fifteen miles offshore, even when the dominant drift is directly seaward. In spite of evident huge mortality the supply of neritic larvae dispersed alongshore seems to be sufficient to maintain large bottom populations wherever environmental conditions permit them to exist.

PRODUCTIVE AND UNPRODUCTIVE AREAS

There is a very great difference in the relative productivity of different areas. It is probable that the greater part of the pelagic population of the Gulf of Maine and Bay of Fundy originates in the coastal region west of Mt. Desert Island. Along the coast east of this point, and including the Bay of Fundy, immigrant adults of both invertebrates and fish mature and spawn, but most of the eggs either fail to develop or die soon after hatching. The local population, often surprisingly large, consists mainly of immigrants arriving as juveniles or adults.

In the present instance temperature combined with turbulence seems to be the limiting factor to successful development. It is during the propagation season from March to September that regional physical and resultant biological differences are greatest. A rather complete stratification of the water mass appears to be essential for successful reproduction of many boreal species. Adults favoring relatively cold water and larvae requiring higher temperatures for normal development encounter these conditions in the western part of the Gulf. The observed descent of larvae to levels of low temperature by day and the rise of adults to warm surface water at night indicate clearly that all can apparently survive temporarily the most extreme conditions existing in the region, provided that there can be periodic access to water within the required thermal range. In turbulent areas with relatively homogeneous water, such as the Bay of Fundy and eastern Maine coast, where one finds neither warm surface nor cold bottom water, environmental conditions are not favorable either for young or adult

zooplankton. It may be that violent mechanical mixing might account for the scarcity of certain boreal species of fossils in areas where the character of the bottom and probable depth would seem to be favorable.

TEMPERATURE

It is evident from the observations already made that of all factors controlling marine life, the influence of temperature is the most readily detectable. Particularly in regard to the pelagic populations, biological processes and distribution are most closely correlated with this factor. Pelagic species usually have a more restricted thermal range than their benthonic relatives, which factor in boreal waters results in a seasonal progression of changes in the composition of the plankton. The sessile benthonic populations are closely attuned to the average temperature range in their particular locality. This is indicated by the destruction of whole communities in certain areas during cold winters when the temperature of the water remains for some time a few degrees below the usual minimum.

Fortunately the destruction of bottom invertebrate populations in neritic waters by temperature is rather uncommon. Even rarer is destruction of this type in offshore bottom communities, but even this is possible, as evidenced by one particularly disastrous occurrence in the latter part of the past century. On that occasion unusually cold water apparently displaced the warm water of the Gulf Stream adjacent to the slope. Off the New England coast immense numbers of dead tile fish were found floating at the surface, and bottom collections of the following year indicated that a considerable part of the benthonic invertebrate population had also been destroyed.

TROPICAL IMMIGRANTS

In the open ocean destruction of pelagic organisms takes place continuously on an enormous scale. The Gulf Stream forms a highway over which are transported northward into boreal waters a very large and varied fauna of tropical vertebrates and invertebrates. None of these establish themselves in colder latitudes. Some are apparently killed outright. Others become widely distributed in coastal waters and die only when the temperature drops in the autumn. Still others survive for considerable periods as indicated by the records of *Salpa* in the Bay of Fundy in December, *Lepas* off western Greenland, and frequent tropical stragglers off Iceland and Norway.

ARCTIC IMMIGRANTS

Arctic immigrants are transported south in the Western Atlantic in large numbers by the Laborador Current. A portion of these are no doubt killed upon coming in contact with the Gulf Stream. Others pass along the Nova Scotian coast and, during the cold months, into the Gulf of Maine where they often survive until spring. Neither arctic nor tropical forms propagate successfully in boreal waters as a rule, so that at best it is merely a case of delayed destruction.

It is impossible to estimate the extent of this mortality in boreal waters, but its importance is emphasized by the fact that it never ceases. Incidentally in the past there were no doubt occasional pelagic migrants of the same sort drifting far beyond the boundaries of their normal ranges. In tracing faunal regions, therefore, the paleontologist would do well to place greatest emphasis on benthonic species. Even among the latter there are a few species which at the present time are found well beyond their limits of successful propagation. On the European coast larvae of *Cucumaria frondosa*, a holothurian, are transported in a southerly drift to temperate regions where they survive. Not being able to reproduce in the warmer waters, restocking takes place from breeding areas farther north. Cases of this sort however appear to be rather uncommon.

Although the methods of the paleoecologist and the marine biologist must necessarily be different, their objects are the same, and it is hoped that they may become more closely associated.

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BOTTOM CONDITIONS IN A TIDAL LAGOON[1]

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ABSTRACT

The arcuate shoal in Barnegat Bay, New Jersey, west of the inlet is described as a tidal delta. The shoal waters on the delta support a flourishing marine fauna consisting largely of pelecypods, gastropods and crustaceans.

Presence of a micro-fauna, mostly Foraminifera, on the surface and through the buried portion of the delta lead to the assumption that the environment in the lagoon has been similar to the present environment throughout the depositional history of the delta. An abundant macrofauna now lives in the lagoon but is not preserved in the delta sediments. This suggests rapid destruction of the hard parts after burial. No conclusive explanation is offered for such destruction but the author points out that such phenomena may be as common in ancient seas as at present and that the fossil content of a formation may, therefore, be an untrustworthy indication of the environment at the time of deposition.

Black, fetid, organic matter rich in iron sulphide is described as a minor constituent of the surface layers of the delta and a major constituent of gelatinuous black muds found in small, isolated areas on the delta. The mud is similar to many ancient black shales and to mud on the bottom of the Black Sea. Its origin and distribution on the delta is discussed.

Barnegat Inlet is a tidal inlet on the coast of New Jersey about forty miles south of Sandy Hook, serving as the only direct connection between the ocean and Barnegat Bay, part of a long coastal lagoon.

As is commonly the case at a tidal inlet on a shoreline of emergence, deltas have been deposited both seaward and landward of the inlet. The tidal delta in Barnegat Bay (Figure 1) was surveyed in detail (1932) to determine how it was deposited, its composition, history and importance in the broad field of shoreline geology. The study[2] involved the collection and analysis of nearly fifty bottom samples and about thirty cored samples of sediment.

The present paper describes certain of the sedimentary data which bear upon paleoecology and stratigraphy, in the expectation that comparison of contemporaneous shore conditions may throw light upon problems of the geologic record.

SEDIMENTARY AND FAUNAL EVIDENCE

The Barnegat delta is composed almost entirely of medium to fine grains of quartz sand. The material is beach-drifted debris which was swept into the lagoon by flood tidal currents and deposited in the quiet water.

The deposit is characterized by great uniformity in that heavy min-

[1] This paper was contributed to a symposium on paleoecology held at the meeting of the Paleontological Society in December, 1933. Manuscript received February 15, 1934.

[2] Lucke, John B., A study of Barnegat Inlet, New Jersey, and related shoreline phenomena: *Shore and Beach*, vol. 2, No. 2, pp. 5–54, 1934.

eral content averages less than three per cent and the silt-clay fractions are correspondingly low. As might be expected in a waterlaid deposit, grain size decreases steadily from the inlet landward. The cores (Figure 1) indicate little vertical change to a depth of thirty feet below the delta surface. Except for slight concentrations of silt and organic debris in the surface foot or two of the delta little or no stratification is apparent. This is in accord with other deposits formed of extremely uniform ma-

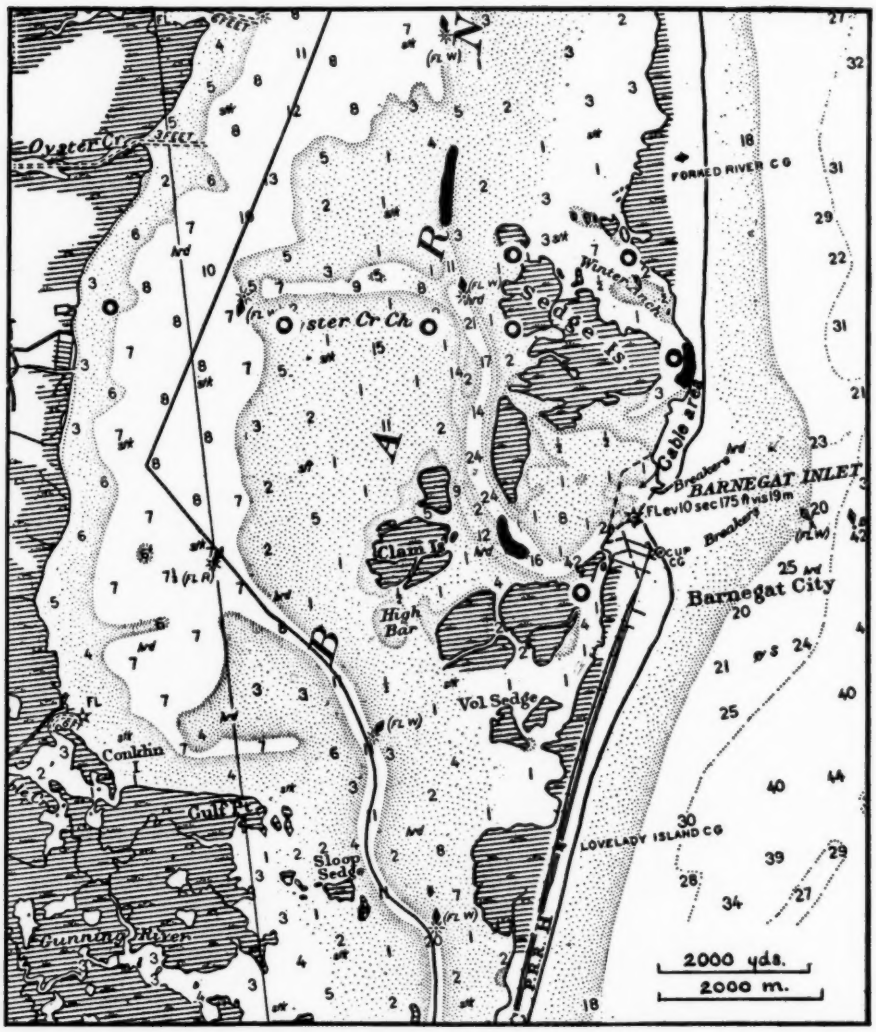


FIG. 1. Chart of the Barnegat Inlet region showing two tidal deltas. Circles mark cores in the delta; black areas represent concentrations of black, organic muds.

terial, such as marine sands and loess beds.

Life in the shoal water (average depth two feet) near the inlet is typical of shallow marine conditions. The tidal flats abound in the hard clam *Venus*, the soft clam *Mya*, the blue crab *Callinectis* and the king crab *Limulus*. Common but not abundant are hermit crabs, periwinkles, starfish, sponges and various marine worms. Many areas which are partially exposed at low tide are covered with a gelatinous ooze formed partly of algae but largely of eggs of vertebrates and invertebrates. The temperature of shallow pools on these flats often exceeds 90° Fahrenheit and they seem particularly suited to the hatching of eggs, since they are isolated from all predatory animals except the seagulls.

The general picture of the area is that of a flourishing clam flat above which gastropods and crustaceans abound. The natural expectation that the buried fossils within the delta should afford a picture of the life on the delta is not realized. The discussion of this important problem forms a large part of the present paper.

PROBLEMS OF SEDIMENTATION AND FOSSILIZATION

Microfossils.—In a representative suite of both bottom and cored samples examined to determine the age, if possible, of the delta, over a dozen species of Foraminifera were identified. Sandidge[3] described them all as forms living in the Atlantic at the present time. Most of them are cool water inhabitants such as are found off Newfoundland and the New England coast. There was nothing which could be used as a direct means of establishing the age of the delta sediments. Other microfossils included a few ostracods, small gastropods and very young pelecypods. The tiny fossils were not restricted either in depth or in geographic distribution on the delta.

The presence of modern forms in the lagoon to a depth of thirty feet of sediment suggests that the entire deposit is Recent in age and, therefore, that the environment in the lagoon has not undergone any great change throughout the depositional history of the tidal delta.

Macrofossils. — No recognizable fossils were found in the buried sediment of the delta except for occasional calcareous worm-tubes and fragments of hard shell clams. This statement is based upon what may be considered the insufficient evidence of the eight cores (Figure 1), but it seems highly unlikely that these widely separated cores should happen to penetrate eight barren zones in an otherwise fossiliferous formation of wide lateral extent.

The microfossils indicate that the present marine conditions probably obtained throughout the life of the delta. It follows, therefore, that the present abundant *Venus* and *Mya* fauna is the normal condition and has always been present in the lagoon. The flourishing clams probably inhabited the bottom sediments of the

[3] The determinations of the microfossils were made by John R. Sandidge. See publication cited above for illustrations of the species.

delta in former years as well as today.

Scarcity or lack of macro-fossils at depth means that the hard parts, the shells, either were never buried or have been destroyed after burial. The life habit of the periwinkles, mussels, and crabs, which are usually exposed to wave and current action, is likely to result in the removal of their hard parts by rapid currents. Clams, on the other hand, must die in the buried position they assume in life. The hard clam *Venus* lives only a few inches below the bottom, but the soft clam *Mya* is often buried to the depth of eighteen inches. The conclusion that vast quantities of shells are destroyed seems inescapable and the destruction may be caused by various agents. Many shell fragments are clearly remnants that have survived the attacks of boring animals such as worms or sponges. Others may have been attacked by acids derived from the decomposition of the soft parts. The abundance of microfossils, whose soft parts are commonly removed before burial of the tiny shells, lends weight to the latter hypothesis. The somewhat brackish water of Barnegat Bay may favor solution of calcium carbonate, although common sea water is not an active solvent. Whatever causes such wholesale destruction of recently buried shells, the fact of their destruction is apparent in Barnegat Bay and is duplicated in many similar areas at the present time.

The disappearance of large quantities of newly buried shells may well have occurred throughout geologic time. If so, do fossiliferous beds in the geologic column represent the life environments of the animals preserved, or do they merely represent areas favorable to the accumulation of hard parts? The latter may often be true and has not always been considered by students of stratigraphy. The assumption that animals lived in an environment similar to that in which their hard parts are preserved is common in the literature, especially in textbooks. The converse is also popular, that a barren formation of red beds or black shales is barren because the environment at the time of deposition did not support life.

Let us lithify the sediments in Barnegat Bay, uplift the region and dissect the surface to a relief of fifty feet. Outcrops would reveal a fine grained, massive, yellow to gray sandstone. Bedding planes would be absent or indistinct unless a ravine happened to reveal an old channel with its scour and fill stratification. The only clew to the deltaic origin, excepting topography, would be the constant decrease in grain size radially from the site of the old inlet. Except for the microfossils, which might go unnoticed, the sandstone would appear quite barren. It might be classified as marine because of a few shell fragments and the general character of the grains. That the environment during deposition supported an abundant marine fauna would never be suspected.

In a study of paleoecology, therefore, the possibility must be entertained that many barren formations have been robbed of evidence of a luxuriant fauna and that highly fos-

siliferous beds may have been deposited in an environment inhospitable to life.

Black Mud.—Nearly all the bottom samples collected contain some carbonaceous matter of organic origin which emits the odor of hydrogen sulphide associated with active decomposition. The organic material colors the sands gray or black but the dark color rapidly disappears upon exposure to the atmosphere. Thus, the flats exposed at low water are yellow to buff, but are gray to black if the topmost inch or two is scraped away. Similarly, a sample of dark gray, fetid sand will quickly turn yellow and lose its odor upon exposure to the air.

The darkened sands usually comprise only the uppermost two or three feet of the delta beds. A similar distribution of organic matter in an algal lake in Florida led Trask[4] to associate its origin with aerobic organisms. The black color in the Barnegat sediments is in part due to iron sulphide, which characteristically oxidizes upon exposure to the air. Many of the samples, stored in screw-top jars, were covered with a rust-colored scum after standing a few weeks. Iron sulphide is common in black muds of the Black Sea[5] as well as in those of the Florida lake[6] previously mentioned. It is also common to many black fine grained rocks of various ages. Both siderite and pyrite are found in the black, bituminous Marcellus shale (Devonian) of New York, and pyrite is present also in the black Genese shale (Devonian) of the same region. Marcasite and pyrite are abundant in the black Magothy clay (Cretaceous) of New Jersey.

In three small areas on the Barnegat Delta (Figure 1, black areas) the organic matter is so strongly concentrated that it forms a jet black, highly gelatinous ooze which freely liberates hydrogen sulphide. The sediment from these areas is quite similar to the older formations cited above. The easternmost of the three deposits is in a closed depression. The others are in present delta channels, and all of them are surrounded and underlain by quartz sands. The smallest mud deposit is but two feet thick and the others are only slightly thicker. Sampling devices invariably encountered gray and finally clean yellow sands below the black muck.

The problem of the origin and distribution of such muds may have a bearing upon fossilization. The only organisms found in the slime were worms and mussels. Although the muds support no clams at the present time, the percentage of organic matter is high in areas where living clams are abundant. It seems probable that production of the toxic muds may partially, at least, be related to the decay of the dead clams. The presence of the toxic material may also play a part in the destruction of calcium carbonate shells.

The localized areas of black mud on the delta owe their existence partly to the depressions in the bottom. This is true of many similar deposits

[4] Trask, Parker D., *Origin and environment of source beds of petroleum*, p. 166, 1932.
[5] Trask, Parker D. *op. cit.*, p. 150.
[6] Trask, Parker D. *op. cit.*, p. 166.

in bays and shallow seas.[7] The question of whether the black muds were originally produced in their present locations or were merely deposited in settling basins cannot be answered.

If the earlier assumption is true that the delta environment has not changed throughout its history, one should expect to find, by sinking cores, buried lenses of black mud representing areas of accumulation on an earlier, smaller delta. Nothing of this kind was encountered by the eight cores sunk in the region. Indeed, no organic matter of any kind contaminated the buried beds of the delta. As in the case of the clam shells, the black material either was not buried, or was removed after burial. Trask[8] suggests that no one of the cores happened to hit the relatively small lenses of organic mud. He agrees with the author that early deposits of this type were almost certain to have been produced and buried.

The alternative hypothesis, previously mentioned, is that the black particles were destroyed or removed. Four points may favor this view: (1) The organic matter is in very finely comminuted particles, much smaller than the quartz grains associated with it; (2) the sediment of the delta, recently deposited, is largely well-rounded beach sand, the porosity of which must be very high, especially when unconsolidated; (3) organic material is concentrated in the surface layers of the delta; (4) inorganic particles of silt-clay grade are also concentrated near the surface over the greater portion of the delta.

This assemblage of facts suggests that after deposition of the sands with their small percentage of silt, clay, or organic particles, the finest grains may have percolated upward through the large interstices between the loosely compacted, well rounded sand grains. Direct evidence for a rising current of water in the delta sands is not available but the suggestion is strong.

Knowledge of marine biology and the related sciences which are vital to the solution of the problems presented is not yet far advanced. The details of the Barnegat Bay conditions may aid in solving these problems and the data presented may be useful in comparisons of contemporaneous sedimentation with the records of ancient shorelines.

CONCLUSIONS

The principle of projecting present day processes into the past to reconstruct the geologic history of the earth is one of the guiding principles of the science. The reconstruction of a picture of what the Barnegat sediments would look like after they had become hard rock clearly indicates that caution must be used in the interpretation of the geologic records. The fossil content of a rock may be a significant indication of how that rock was deposited and what the environment was like at the time of deposition, but the author emphasizes the fact that this is only a possi-

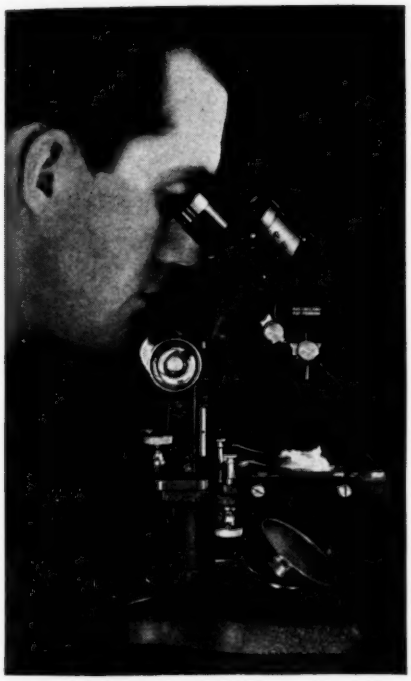
[7] Trask, Parker D., *op. cit.*, p. 120.
[8] Trask, Parker D. Personal communication.

bility. It may not even be likely, and it surely is not necessarily, the trustworthy evidence of ancient conditions which it has often been considered. The almost complete lack of fossils in the Barnegat sediments, if repeated in ancient sediments, makes one wonder why so many fossils have been found and how many generations of animals may have lived in the geologic past without leaving any record of their existence.

PALEONTOLOGICAL NOTES

MEETING OF THE SOCIETY OF ECONOMIC PALEONTOLOGISTS AND MINERALOGISTS

The next annual meeting of the Society of Economic Paleontologists and Mineralogists will be held at the Allis Hotel, Wichita, Kansas, March 21–23, 1935. Members of the Paleontological Society are very cordially invited to participate in these meetings. Titles of papers that may be offered should be transmitted, accompanied by abstracts, to Gayle Scott, Texas Christian University, Fort Worth, Texas, on or before February 15.



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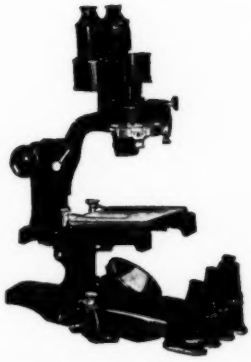

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